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Carbon Assessment in Boreal Wetlands of Ontario

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Executive Summary

Understanding terrestrial, freshwater, and marine carbon (C) dynamics is a very challenging but important political and scientific issue. Locating the sources and sinks of carbon dioxide (CO_2) and methane (CH_4), as well as understanding their spatial and temporal distributions are critical to predicting C responses to management innovations or climate change. This emerging issue has major international economic and political implications. Wetlands are believed to be key components of the atmospheric C balance and thus have been a central point of research for the past 2 decades. This has greatly reduced uncertainties in understanding wetland C cycling. However, critical knowledge gaps regarding sources and sinks remain to be understood before adequate predictions relating wetlands to regional, national, and global C budgets are possible.

Multi- and inter-disciplinary research are required to improve the understanding and predictions of wetland C biogeochemistry at local, regional, national, and global levels. Specifically, critical information that is needed for Ontario includes (1) more comprehensive wetland inventories; (2) standard monitoring methods that are consistent with national and international initiatives; (3) monitoring and research sites that are selected to better represent the entire wetland land area; (4) mechanisms to extrapolate monitoring and research results to landscape, regional, and national scaling; (5) more complete measurements of C pools in peat, litter, and vegetation (both above- and belowground); (6) more complete measurements of C input and output; and (7) more complete understanding of C biogeochemistry.

Wetlands are defined here as any area of land that is saturated with water long enough to promote wetland or aquatic processes as indicated by poorly drained soils, hydrophytic vegetation, and various kinds of biological activity adapted to a wet environment as defined in the Canadian Wetland Classification System (Zoltai et al. 1988). Thirty percent of Ontario's boreal landscape is classified as wetland (Tarnocai et al. 2000), of which 95% occurs as peatlands (wetlands with peat depth $\geq$ 40 cm). This report reviews the literature on C cycling in northern wetlands, with a focus on peatlands, in the context of C assessment in boreal peatlands of Ontario.

A number of excellent reviews have been published recently on wetland C cycling. Those reviews have discussed peatland C budgets (Gorham 1991), forest management effects on wetland C cycling (Trettin et al. 1995), general climate change effects on C cycling (Moore et al. 1998), peatland C and the Kyoto Protocol (Roulet 2000), net primary production (NPP) (Campbell et al. 2000), CH_4 emissions (Bartlett and Harris 1993, Segers 1998), CH_4 production and oxidation (Schink 1997, Le Mer and Roger 2001), organic matter decomposition (Johnson and Damman 1993, Aerts et al. 1999), and basic peatland C cycling dynamics (Blodau 2002). This report will complement those wetland C reviews by focusing on the interactions between vegetation and hydrology and their effects on regulating peatland C cycling and budgets at both local and regional scales in the boreal zone of Ontario. The report presents and discusses information and suggests areas of research that span multiple spatial and temporal levels related to uncertainties in peatland C cycling. This report summarizes the state-of-the-knowledge in peatland C dynamics, identifies critical research gaps, and presents research that is currently being conducted (but in its infancy) to improve the ability to assess C in Ontario's peatlands. Information from the report can also be used to help define the role of Ontario's peatlands in national and global C cycles and budgets.

Knowledge of the spatial and temporal patterns of peatland sinks and sources for atmospheric C in Ontario is very important. For example, Ontario's boreal forest currently functions as a net source of atmospheric C, likely because of the high fire frequency in the area (Kling et al. 2003). Peatland C

sequestration may fill an important niche that aids in reducing the atmospheric C burden from the boreal forest in Ontario. As such, understanding the role of Ontario's peatlands in C sequestration and the sink/source function of Ontario's boreal landscape is critically important.

The report comprises 5 major sections:

Introduction:

This section introduces the topic of peatland C cycling and the importance of vegetation and hydrologic interactions in its regulation. It also presents components of peatland C budgets, emphasizing the lack of information about a number of these components.

Extent and Types of Wetlands:

This section lists the uncertainties in global estimates of wetland extent and describes the boreal wetland regions and wetland types in Canada including peatlands in Ontario based on peatland inventories for northeastern (Riley 1994) and northwestern Ontario (Riley and Michaud 1987).

Carbon Cycling in Boreal Peatlands:

This section is divided into 7 subsections:

1. *Peatland net primary production and litter decomposition*, which discusses the role of net primary production and litter decomposition in boreal peatlands, emphasizing the role of litter quality and roots on C cycling

2. *Peat accumulation and carbon sequestration*, which describes the process and controls peat accumulation and C sequestration.

3. *Carbon storage in Ontario's boreal peatlands*, which uses data from peatland inventories of Riley (1994) and Riley and Michaud (1987) in association with published literature on Ontario's boreal and subarctic peatlands to develop initial C storage, C fluxes in Ontario's peatlands, and C transport from transient to long-term storage. The results from Riley's (1994) and Riley and Michaud's (1987) inventories indicate a dominance of forested peatlands (i.e., conifer swamps) in northeastern and northwestern Ontario. However, limited information is available on the C cycling dynamics of conifer swamps in Ontario: a situation in dire need of correcting.

4. *Carbon cycling dynamics*, which discusses the role of oxidation-reduction (redox) reactions as the major driver of peatland C cycling.

5. *Methane*, which discusses the importance of peatlands to atmospheric loading of CH_4, its production in, and emission from northern peatlands. Notably Ontario has the second lowest CH_4 efflux in the Northern Hemisphere. A number of abiotic and biotic interactions are suggested as causes of this phenomenon, with organic matter quality likely a major driver of the low CH_4 production rates reported for Ontario's peatlands. Also, CH_4 emission rates from fens, bogs, and conifer swamps, and subforms within each peatland type in Ontario are calculated based on the peatland inventories of northeastern (Riley 1994) and northwestern (Riley and Michaud 1987) Ontario and published CH_4 emission rates.

6. *Carbon dioxide*, which discusses the importance of peatlands to atmospheric CO_2 concentrations and measures of CO_2 exchange in peatlands. Three methods commonly used to estimate peatland net ecosystem productivity (NEP) are presented. Measures of the net ecosystem exchange (NEE) of CO_2 in North American peatlands and tundra are also presented. Net ecosystem exchange of CO_2 has been studied only on few peatlands in North America. The values of NEE published for bogs

indicate that they are net C sinks, whereas NEE of fens indicate that they can be either a net source or sink of atmospheric C.

7. *Climate change and peatland carbon cycling*, which discusses the potential roles of temperature and precipitation shifts on peatland C cycling and sink/source relationships.

The limited information currently available indicates that peatlands in the southern portion of the boreal forest of Canada function more frequently as a net CO_2 sink compared to peatlands occurring in the northern portions. This may be due to a longer growing season in the southern compared to northern boreal forest.

The link between phenological stage of peatland plants and climatic conditions is discussed in relation to CO_2 sink/source strength. However, data are lacking on annual measures of CO_2 exchange in North American peatlands, an area that needs more study. Thus, long-term monitoring needs to be expanded to provide higher quality data for refining climate change and peatland C sequestration models.

Scaling Peatland Carbon:

This section discusses different approaches used to scale peatland C to landscape, regional, and global levels, focusing on CO_2 and CH_4. Bottom-up techniques, that is, the emission factor approach and modelling, are presented.

1. *Emission factor approach* derives estimates of trace gas emissions by combining measurement data with geographical and statistical information about ecosystem processes using the area of the functional unit (e.g., land cover, topographic position, management unit) and the emission factor (e.g., g CO_2-C m^{-2} yr^{-1}). Using this approach, both the stratification scheme of the functional unit and reliability of the emission factor determine the accuracy of flux estimates. Four related studies published in the literature are highlighted.

2. *Modelling* is used to scale peatland C and the contribution of peatland C cycles to Canada's C budgets. The modelling approach being developed for Canada, which couples process- and semi-empirical-based models of peatland C cycling to the Canadian Land Surface Scheme (CLASS) and subsequently to the Canadian Coupled Climate Model (C^3M), is discussed.

Summary and Recommendations:

This section reiterates the land area, estimated C storage, and CH_4 efflux of Ontario's boreal peatland resource. It also summarizes the knowledge gaps remaining before accurate assessments of peatland C budgets are possible. These include:

- the timing of snowmelt, soil thaw, precipitation patterns, and temperature patterns on CO_2 and CH_4 cycling in Ontario's peatlands;
- the interactions of organic matter quality and climatic variables (i.e., temperature, and precipitation/water table depth) in regulating C sink/source strength of peatlands;
- climate change effects on peatland succession, litter quality and decomposition rates, and how these relate to C budgets.

Additional information is also required about the C flux at the peatland surface/atmosphere/groundwater/surface water interface. One-fourth or more of the soil respiration (i.e., CO_2, CH_4) can be transported to surface waters draining peatlands. A more thorough understanding of the cycling of C transported to aquatic systems is also needed. This will support more accurate assessments of the C balance of boreal landscapes in Ontario.

The Ontario Ministry of Natural Resources (OMNR) should be actively involved in addressing these research areas. An infrastructure of research sites currently exists across Ontario that can be used to begin addressing identified research priorities. For example, peatlands in the Hudson Bay Lowlands, which were part of the Northern Peatland Study in the late 1980s and early 1990s, the Mer Bleue Peatland Complex near Ottawa under Fluxnet-Canada, the Walley Creek forested peatland site near Cochrane, the riparian peatland study site near White River and the Experimental Lakes Area near Kenora, can serve as the initial infrastructure of study sites to begin a province-wide network for peatland C cycling research and monitoring. The Ontario Forest Research Institute can be the lead for the forested peatland portion using the Walley Creek and White River study sites, and collaborate with researchers at Mer Bleue and the Experimental aLakes Area.

The priorities should be to develop C budgets and determine the quality of litter and peat at each of the research sites. The site network can serve as gradients for both climate (temperature and precipitation) and geology (lacustrine and marine deposits, Precambrian Shield, Ordovician Limestone). Results obtained from this network can be coupled with work currently being conducted in Ontario and Canada related to scaling of peatland C dynamics and the importance of peatlands in C cycling in boreal landscapes. Also, this network would be ideal to support the development of standard methods for studying C cycling in northern peatlands. The Ontario Forest Research Institute is already participating in a bi-national collaboration between Canada and the United States to investigate wetland C dynamics in forested wetlands within the region.

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Introduction

Wetlands cover only about 3% of the Earth's surface, but they are estimated to store about one-third (455 Pg C; 1 Pg = 10^{15} g) of the terrestrial soil carbon (C) pool and represent 60% of C currently stored in the atmosphere (Aselmann and Crutzen 1989, Gorham 1991). Northern wetlands sequester C at rates estimated between 0.03 and 0.29 g C m^{-2} d^{-1}, with an average rate of about 0.15 to 0.19 g C m^{-2} d^{-1}. This translates into 5 to 85 g C m^{-2} yr^{-1} or a total sequestration rate of 76 Tg C (1 Tg = 1 million tons) annually for long-term storage as peat in North American wetlands (Gorham 1991). Thus, northern wetlands may be significant in terms of the so-called 'missing sink' of global C (Houghton et al. 1998).

Wetlands are defined here as any area of land that is saturated with water long enough to promote wetland or aquatic processes as indicated by poorly drained soils, hydrophytic vegetation, and various kinds of biological activity adapted to a wet environment as defined in the Canadian Wetland Classification System (Zoltai et al. 1988). There are many types of wetlands (divided into non-peat-forming and peat-forming categories), many ecological types within these wetland types, and further subdivisions within ecological types. Peatlands (peat-forming wetlands) differ from non-peat-forming wetlands by a combination of interrelated hydrologic, chemical, and biotic factors (Mitsch and Gosslink 1993) that result in low organic matter decomposition rates relative to plant production, allowing for the accumulation of peat (Clymo 1984).

Ontario's landscape consists of 312,780 km^2 of wetlands, which represents 30% of Ontario's land area (Tarnocai et al. 2000). Ninety-three percent of the wetland area in Ontario is classified as peatlands, much of which occurs in the topographically low-gradient areas of the Clay Belt and Hudson Bay Lowlands regions. But, Ontario's peatlands are widely dispersed across the province (Riley and Michaud 1987, Riley 1994, Tarnocai et al. 2000). Significant amounts of peatlands also occur along the shorelines of lakes and streams and in valley bottoms; thus peatlands are important for landscape C transfer in Ontario.

Peatlands are subdivided hydrologically into fens, which are geogenous systems affected by mineral soil waters (groundwater or surface water) that may (rich fens) or may not (poor and intermediate fens) be rich in mineral elements, and bogs, which are ombrogenous, receiving their surface water predominately from precipitation (Vitt et al. 1994). Bogs generally have a relatively low water table, greater insulation capacity, and low thermal conductivity of the relatively dry organic layer compared to fens.

Vegetation communities also differ between boreal bogs and fens. In boreal and subarctic bogs of North America, various *Sphagnum* species dominate the moss layer, ericaceous shrubs dominate the shrub layer, and black spruce (*Picea mariana*) dominates the tree layer (Zoltai et al. 1988). In contrast, dominant vegetation on fens includes brown mosses (rich fens), *Sphagnum* mosses (poor fens), or mixtures of *Sphagnum* and brown mosses (intermediate fens) in the moss layer; sedges (Cyperaecea) in the herbaceous layer (rich fens), deciduous shrubs (rich fens), ericaceous shrubs (poor fens), or a combination of both (intermediate fens) in the shrub layer and tamarack (*Larix laricina*) and/or birch (*Betula* spp.), which may (poor and intermediate fens) or may not (rich fens) occur in association with black spruce in treed or forested fens.

Peatlands are a vital component of northern landscapes and are composed of a broad range of geomorphic and biological systems. These systems create complex spatial and temporal patterns of peatland structure and C cycles (Vitt et al. 1994, Halsey et al. 1997). On a regional scale, climate (temperature and precipitation) and physiography (bedrock geology and underlying mineral soil texture) are important drivers of C cycling (Belyea and Clymo 2001). At the local level, vegetation community structure and its net primary production (NPP) and hydrology are the major drivers of peatland C cycles (Camill 1999). Therefore, it is critical to understand the relationships among vegetation, hydrology and C cycles to improve understanding of peatland C dynamics.

Because northern peatland ecosystems exist as the result of multiple sensitive interactions between hydrology and vegetation, they are responsive to perturbations in climatic conditions, drainage, peat harvesting, and forest harvesting (Roulet et al. 1993; Trettin et al. 1995; McLaughlin et al. 1996a, 2000; Roulet 2000; Laiho et al. 2003). Those disturbances could significantly affect local and regional hydrology, floral assemblages, ecosystem productivity, and C flux, subsequently altering the ability of northern peatlands to act as effective C sinks. The C sink/source function in peatlands is the product of: (1) hydrologically driven mass flux of both organic and inorganic C through a system, (2) the delivery of

organic C to the peat by vegetation as root exudates and fresh litter, (3) the transformation of organic and inorganic C by various aerobic and anaerobic microorganisms, (4) atmospheric uptake of CO_2, and (5) organic matter decomposition and transport of C dioxide (CO_2) and methane (CH_4) through the peat profile.

Peatland vegetation and hydrology are not mutually exclusive in their influences on C cycling. Hydrology and vegetative composition control oxidation-reduction (redox) potential of the system, which is the major driver of peatland C cycling through its effects on soil microbial populations and activities, and gaseous and solution C transport through soils (Schlesinger 1991, McLaughlin et al. 1994, Fiedler and Sommer 2000). A stable water table results in anoxic (reducing) conditions and the production of nitrous oxide (N_2O), hydrogen sulfide (H_2S), and CH_4 gases. A fluctuating water table, however, allows organic material to be more completely oxidized, reducing N_2O, H_2S, and CH_4 emissions, and may not promote accumulation of peat within the system (Clymo 1984).

Carbon cycle and budget components for peatlands include inputs, outputs and storage (Figure 1). However, published and available data to construct comprehensive peatland C budgets are limited (Waddington and Roulet 2000). Moore et al. (1998, 2002) have developed a preliminary C budget for the Mer Bleue bog near Ottawa, Ontario (Figure 2). This tentative C budget indicates the Mer Bleue bog may sequester about 70 g C m^{-2} yr^{-1} (Moore et al. 2002). Trettin et al. (1995) presented a C budget for northern forested wetlands (Figure 3). This budget was developed using published data for northern forested wetlands across the Northern Hemisphere and represents the range of available data. As can be seen in both Figures 2 and 3, most of the C in both bogs and forested wetlands is stored in peat.

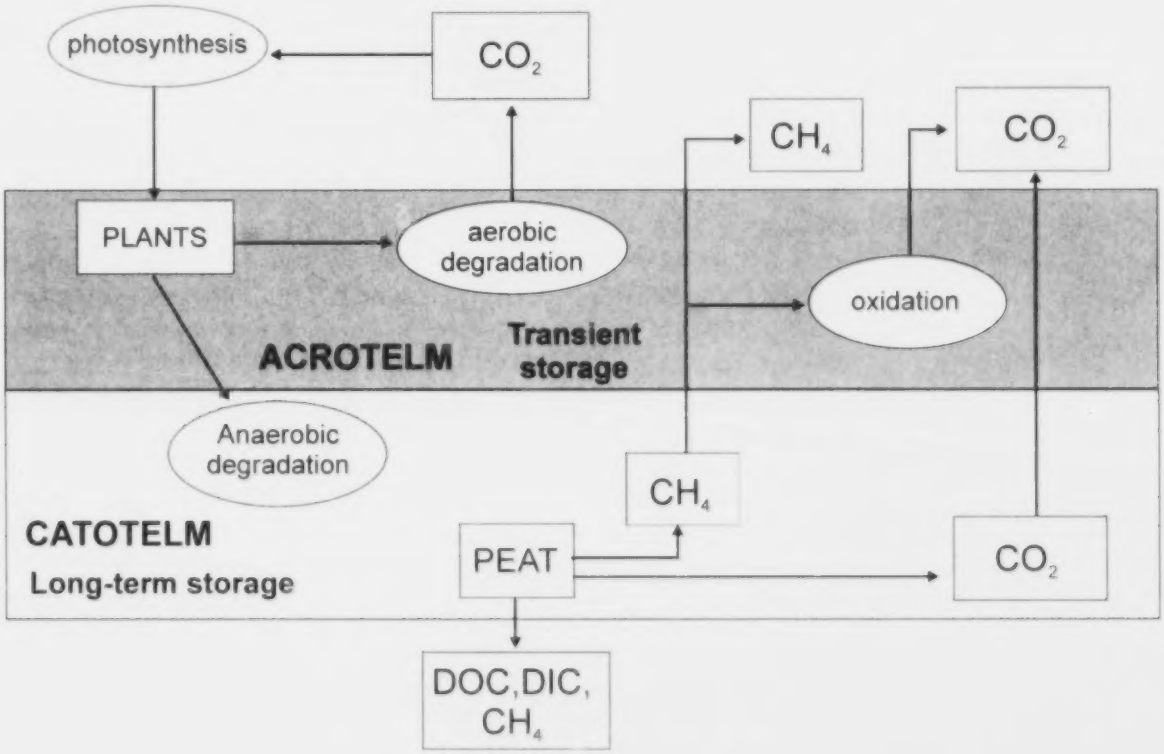


Figure 1. *Peatland carbon cycle (acrotelm represents oxidized region of peat and catotelm represents anoxic region of peat) (adapted from Brown 1998).*

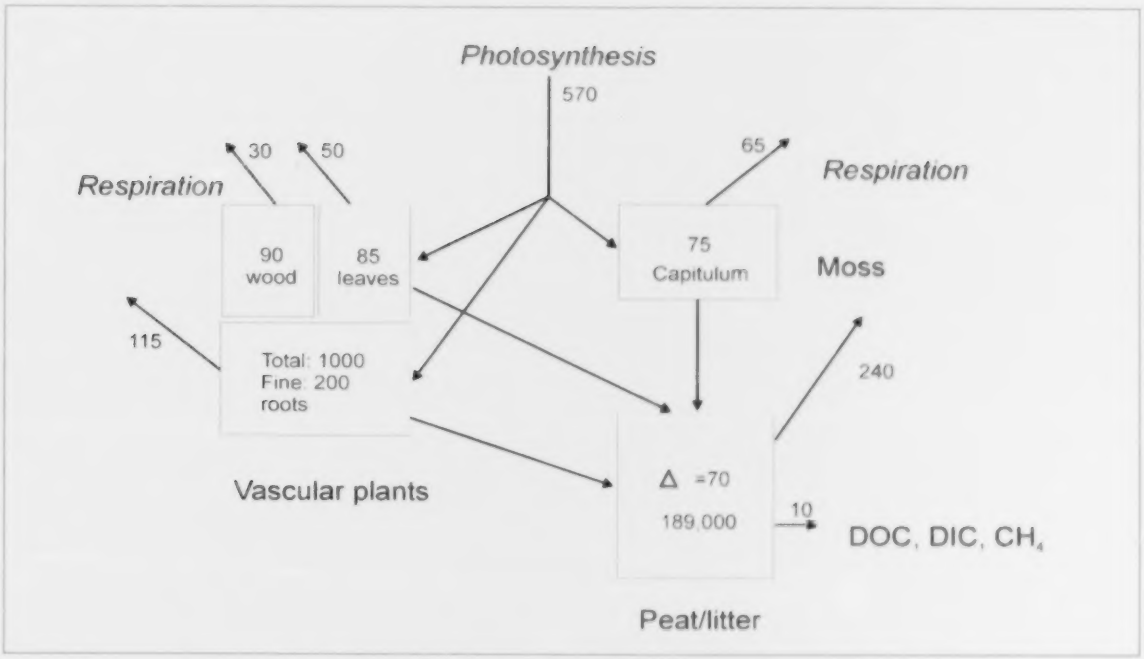


Figure 2. *Tenative carbon budget for the bog section of Mer Bleue peatland complex near Ottawa, Ontario. Stocks are in g C m $^{-2}$ and fluxes are in g C m $^{-2}$ y $^{-1}$ (adapted from Moore et al. 2002).*

The understanding of C cycling in peatlands is improving, but many uncertainties remain at various scales. Multi-dimensional research is required to improve the understanding and predictions of wetland C biogeochemistry at local, regional, national, and global levels. Temporal and spatial understanding of abiotic and biotic wetland characteristics and their interactions on regulating C cycling also needs to be greatly improved. Specifically, critical information required for Ontario includes (1) more comprehensive wetland inventories; (2) standard monitoring methods that are consistent with national and international initiatives; (3) monitoring and research sites that are selected to represent the wetland land area as a whole; (4) mechanisms to extrapolate monitoring and research results to landscape, regional, and national scaling; (5) more complete measurements of carbon pools in peat, litter, and vegetation (both above- and belowground); (6) more complete measurements of C input and output; and (7) more complete understanding of C biogeochemistry. The importance of peatlands to Ontario's, Canada's, and global C cycles is often debated; this will continue until uncertainties are better understood. This report summarizes current knowledge of peatland dynamics, identifies research gaps, presents current research, and suggests new research that is necessary to improve the assessment of C in Ontario's peatlands.

Extent and Types of Wetlands

Global

Globally, many uncertainties exist in the relationship between wetlands and C cycling. A major uncertainty at the global scale is conflicting data regarding the global extent of wetlands (Rodin et al. 1975, Ajtay et al. 1979, Keivinin and Pakarinen 1981, Post et al. 1982, Taylor 1983, Esser 1984, Armentano and Menges 1986, Matthews and Fung 1987, Adams et al. 1990, Riley 1992, Mitsch and Gosselink 1993, Franzen 1994). Reported estimates have included total wetland area, total peatland area, bog area, or swamp area, with estimates of total wetland area ranging from 2.80 x 10^{12} m^2 (Post et al. 1982) to 8.56 x 10^{12} m^2 (Mitsch and Gosselink 1993), total peatland area ranging from 2.38 x 10^{12} m^2 (Taylor 1983) to 5.00 x 10^{12} m^2 (Franzen 1994), area of bogs ranging from 1.21 x 10^{12} m^2 (Esser 1984) to 3.15 x 10^{12} m^2 (Rodin et al. 1975), and area of swamps ranging from 2.10 x 10^{12} m^2 (Matthews and

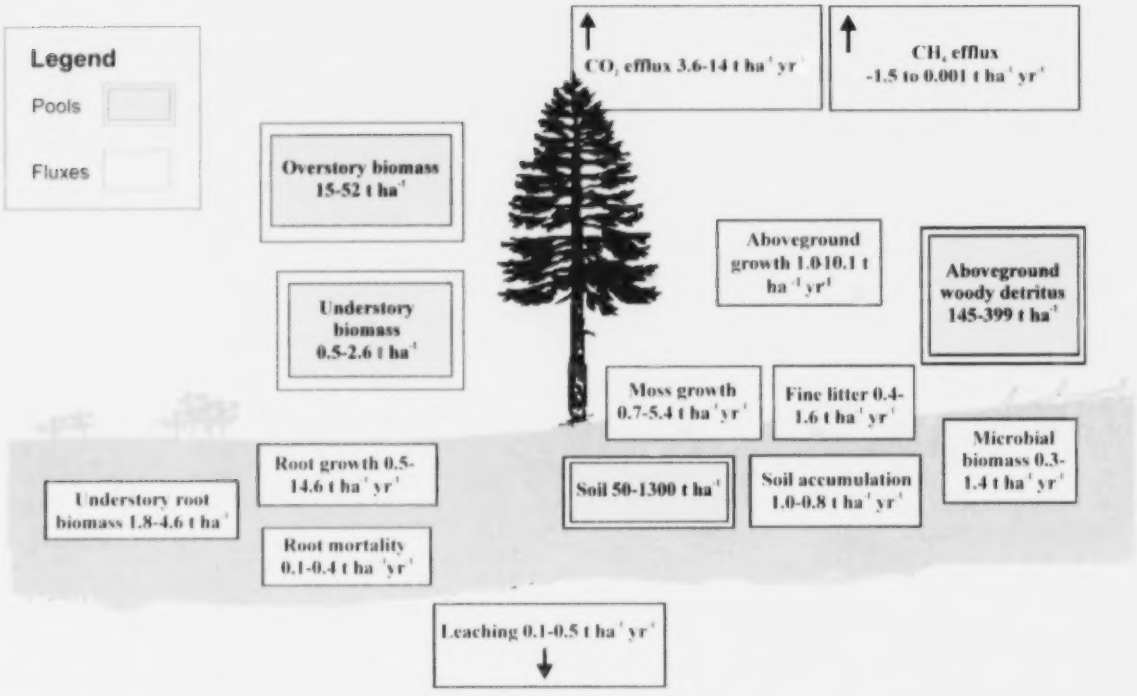

Legend
Pools
Fluxes
CO_2 efflux 3.6-14 t ha^{-1} yr^{-1}
CH_4 efflux -1.5 to 0.001 t ha^{-1} yr^{-1}
Overstory biomass 15-52 t ha^{-1}
Aboveground growth 1.0-10.1 t ha^{-1} yr^{-1}
Aboveground woody detritus 145-399 t ha^{-1}
Understory biomass 0.5-2.6 t ha^{-1}
Moss growth 0.7-5.4 t ha^{-1} yr^{-1}
Fine litter 0.4-1.6 t ha^{-1} yr^{-1}
Microbial biomass 0.3-1.4 t ha^{-1} yr^{-1}
Root growth 0.5-14.6 t ha^{-1} yr^{-1}
Understory root biomass 1.8-4.6 t ha^{-1}
Soil 50-1300 t ha^{-1}
Soil accumulation 1.0-0.8 t ha^{-1} yr^{-1}
Root mortality 0.1-0.4 t ha^{-1} yr^{-1}
Leaching 0.1-0.5 t ha^{-1} yr^{-1}

Figure 3. Distribution and fluxes of carbon in northern forested wetlands (adapted from Trettin et al. 1995).

Fung 1987) to 3.59 x 10^{12} m^2 (Rodin et al. 1975). Major reasons for these differences are terminology inconsistencies and incomplete mapping. Furthermore, development pressures are continually modifying the global extent of wetlands making more frequent monitoring necessary once the current extent is agreed upon (IGBP 1996).

The International Global-Biosphere Programme (IGBP), Global Analysis, Interpretation and Modelling (GAIM)-Data and Information Systems (DIS)-Biosphere Aspects of the Hydrological Cycle (BAHC)-International Global Atmospheric Chemistry Programme (IGACP)-Land Use/Cover Change project (LUCC) held an international workshop in 1996 (IGBP 1996) to identify data and research needs for characterizing the role of wetlands in biogeochemical and hydrological cycles. The purpose of the workshop was to establish functional parameters for assessing wetlands that could more effectively be integrated into trace gas, hydrologic, and other fluxes into regional and global biogeochemical models. They proposed 9 functional parameters for biogeochemical and trace gas characterization that could be used to develop wetland groupings: (1) hydrology, (2) temperature, (3) primary production, (4) vegetation, (5) soil type, (6) salinity, (7) chemistry, (8) transport of organics and sediment, and (9) topography/geomorphology. The IGBP proposed that these parameters would make it possible to subdivide wetlands into functional types in land cover and biome maps to help determine the global distribution and changes (both natural and anthropogenic) in biogeochemical cycling. The latter will be important in prognostic biogeochemical models as they are developed.

According to the IGBP (1996), detailed wetland maps are available for Europe and the United States and regional maps are available for most of the world. However, these maps are almost always static and based on floristics rather than functions. They indicate that it would be beneficial to establish current and ongoing monitoring of wetland extent, with classification based on biogeochemical functions. Such information can now be obtained using remote sensing in conjunction with regional data on soils, climate, and vegetation (Bubier et al. 1997, Thomas et al. 2002).

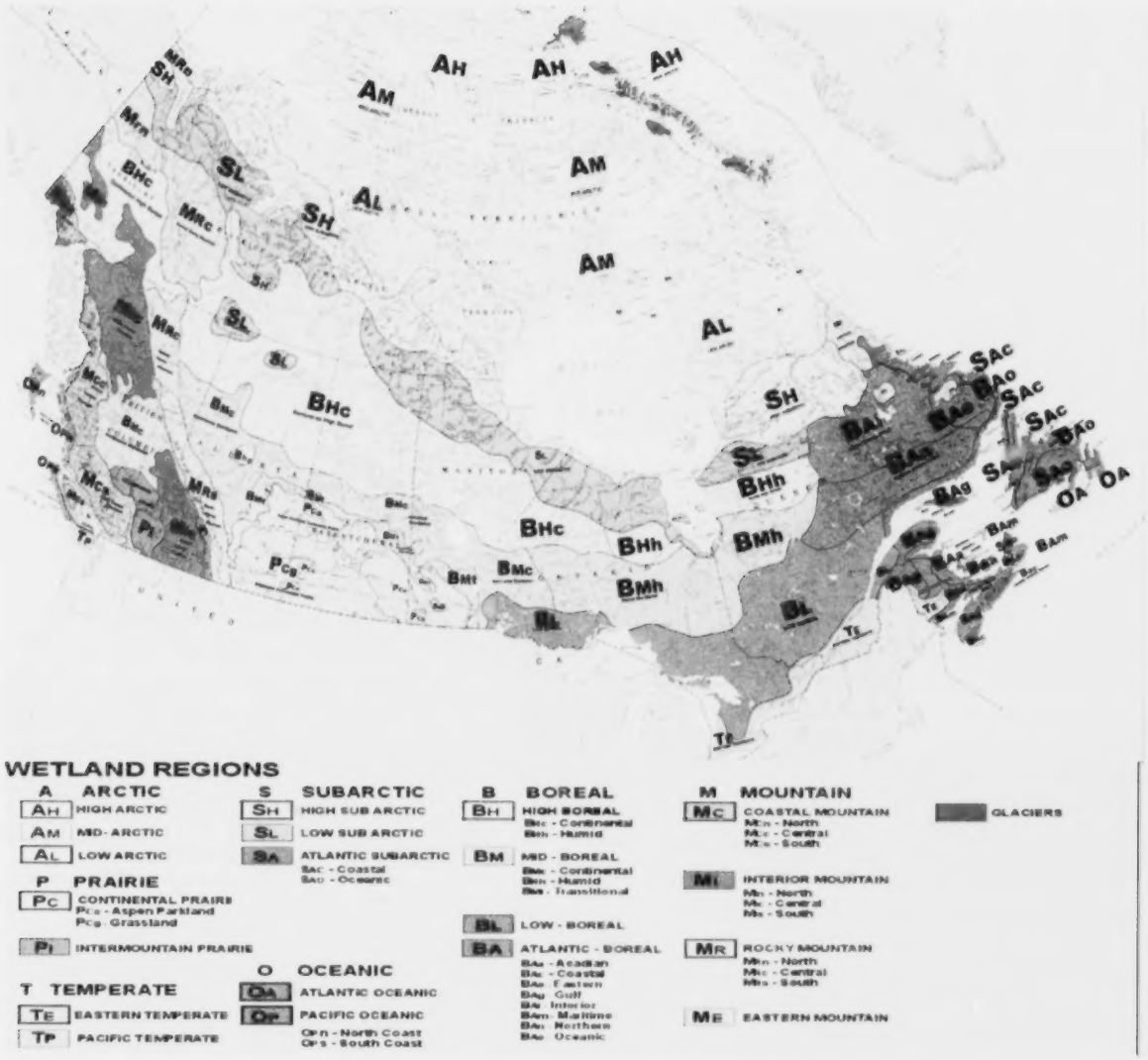


Figure 4. Wetland regions of Canada (adapted from Zoltai et al. 1988).

Boreal wetland regions of Canada

Boreal wetland regions extend across Canada at mid-latitudes. Boreal wetlands are characterized by coniferous forests and cover about 3,034,000 km^2 in Canada (Zoltai et al. 1988). The highest density of wetlands in Canada occurs in the boreal continental region, extending from Alberta to Ontario, with an average of 40 to 50% of the land surface covered by peatlands (Kuhry et al. 1993). In Ontario, the land surface cover of peatlands is about 30% (Tarnocai et al. 2000).

Canada has 4 major boreal wetland regions: (1) Atlantic Boreal, (2) High Boreal, (3) Mid-Boreal, and (4) Low Boreal (Zoltai et al. 1988) (Figure 4). All but the Atlantic Boreal (which will not be discussed in this report) occur in Ontario. For a description of the Atlantic Boreal Wetland Region see Zoltai et al. (1988). The High Boreal Region is subdivided into Continental High Boreal and Humid High Boreal Subregions. The former occurs from northwestern Ontario through British Columbia and into the Northwest Territories. The Humid High Boreal Subregion is restricted to areas of northeastern Ontario and northern Quebec. The

WETLAND REGIONS

A ARCTIC
S SUBARCTIC
B BOREAL
M MOUNTAIN
P PRAIRIE
O OCEANIC
T TEMPERATE

Figure 4

Boreal wetland regions of Canada

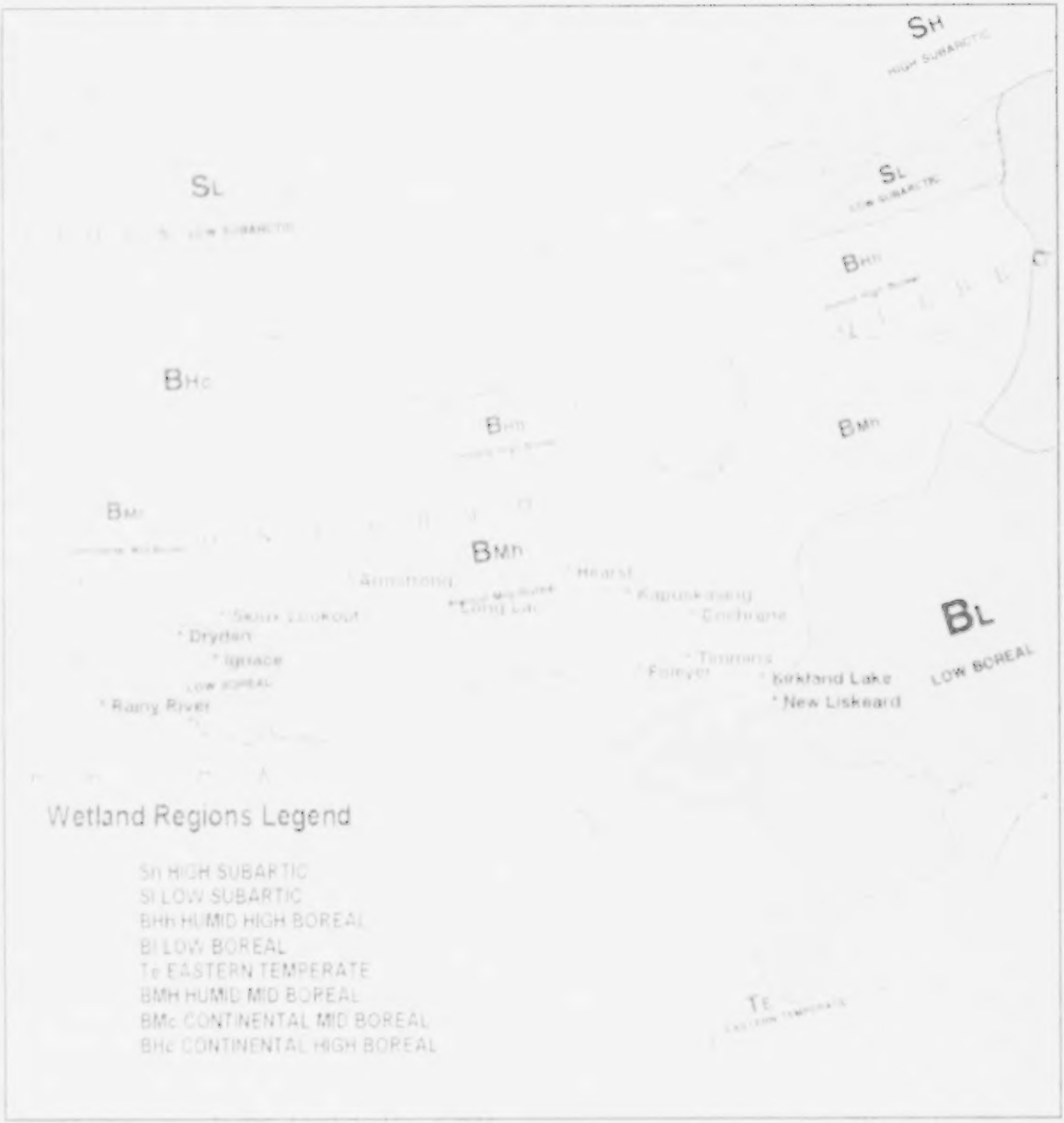

SH
HIGH SUBARCTIC
SL
LOW SUBARCTIC
SL
LOW SUBARCTIC
BHc
BMh
BMh
BMh
BMh
Armstrong
Hearst
Kapuskasing
Ignace
Dryden
Rainy River
Timmins
Foleyet
Kirkland Lake
New Liskeard
BL
LOW BOREAL
Wetland Regions Legend
Sh HIGH SUBARTIC
Sl LOW SUBARTIC
BHh HUMID HIGH BOREAL
Bl LOW BOREAL
Te EASTERN TEMPERATE
BMH HUMID MID BOREAL
BMc CONTINENTAL MID BOREAL
BHc CONTINENTAL HIGH BOREAL
TE

Figure 4. [illegible]

Figure 5. Boreal wetland regions of Ontario (adapted from Zoltai et al. 1988).

Mid-Boreal region is divided into 3 subregions: the Continental Mid-Boreal, the Humid Mid-Boreal, and the Transitional Mid-Boreal. The Continental Mid-Boreal Subregion extends from northwestern Ontario to eastern British Columbia, whereas the Humid Mid-Boreal Subregion occurs in northern portions of Ontario and Quebec. The Transitional Mid-Boreal Subregion extends from Manitoba into Alberta. The Low Boreal Region occurs in northwestern, northeastern, and southern Ontario, and southern Quebec. Boreal Wetland Subregions that occur in Ontario are Continental High Boreal, Humid High Boreal, Humid High Boreal, Humid Mid-Boreal, Continental Mid-Boreal Subregions, and the Low Boreal Region (Figure 5).

Boreal wetlands in Canada are characterized by cold winters and short, warm summers. Boundaries for boreal wetlands are the average summer position of the arctic frontal zone in the north and the winter position of the arctic frontal zone in the south (Bryson 1966). Because of their position, polar and arctic air masses dominate boreal wetlands during the winter while Pacific and tropical air masses dominate in the summer (Zoltai et al.1988). Two major gradients occur in boreal wetland zones: a north to south increasing temperature gradient and an east to west decreasing precipitation gradient. The occurrence and development of different wetland types reflect this climatic zonation. Broad climatic data for boreal wetlands are given in Table 1.

Boreal wetland types in Canada

Canada's boreal region supports mostly 2 types of wetlands: peat-forming and non-peat-forming. Peat-forming wetlands consist of 2 forms: peatlands and histic-mineral soil wetlands. Peatlands are characterized by at least 40 cm of peat. This is the dominant form in the boreal region of Ontario, and Canada as a whole. Histic-mineral soil wetlands are characterized by a 5- to 40-cm thick peat layer. These wetland types are considered nascent peatlands and are common in the southern part of the boreal zone (Trettin et al. 1995), as well as marsh areas bordering surface water (Zoltai et al. 1988). Areas with less than 5 cm of peat are referred to as mineral soil wetlands and are common in the southeastern region of the United States (Trettin et al. 1995).

The National Wetland Working Group (Zoltai et al. 1988) divided non-peat-forming wetlands into (1) shallow open waters, (2) marshes, and (3) swamps, and divided peatlands into (1) bogs and (2) fens. Shallow, open water wetlands are characterized by aquatic processes, which are generally confined to less than 2-metre depth at midsummer. Marshes are open wetlands dominated by sedges and other monocots and are characterized by large seasonal water level fluctuations, relatively large amounts of water flow, and influence from ground- and/or surface water. Swamps are forested, wooded, or shrubby systems where tree growth is limited by regional climatic conditions and/or seasonally wet conditions. Both marshes and swamps have abundant vascular plant production. However, peat

Table 1. Climatic data for the boreal wetland subregions (average values) (from Zoltai et al. 1988).

Wetland region or subregion[a]	No. of stations	Mean annual temp. (°C)	Mean daily July temp. (°C)	Mean daily January temp. (°C)	Mean no. of degree-days above 5°C	Mean annual precip. (mm)	Mean annual snowfall (cm)
BHc	36	-2.7	15.9	-25.1	1,096.0	404.6	162.3
BHh	2	-3.8	13.0	-23.2	706.8	705.8	259.4
BMc	45	1.7	16.1	-17.4	1,274.0	469.0	167.5
BMh	21	0.8	16.4	-18.6	1,264.3	823.8	273.8
BMt	19	1.2	17.5	-19.6	1,470.0	460.2	121.3
BL	53	3.0	18.1	-14.5	1,604.3	836.4	55.0

[a] BHc = Continental High Boreal, BHh = Humid High Boreal, BMc = Continental Mid-Boreal, BHh = Humid Mid-Boreal, BMt = Transition Mid-Boreal, BL = Low Boreal

accumulation is limited by high organic matter decomposition rates. Non-peat-accumulating wetlands have a poorly developed bryophyte layer associated with relatively high seasonal water level fluctuations and high vascular plant production.

Zoltai et al. (1988) defined and described 13 wetland forms in Canada; characteristic dominant vegetation for these wetland forms is given in Table 2. These wetland forms can be further subdivided into ecological types. Those types are open, shrub, and treed bogs and fens, and forested swamps (Zoltai et al. 1988). A number of microtopographic environments exist within a wetland which affects peat accumulation (Clymo 1984, Clymo et al. 1998). Distinct microtopographic patterns include hummocks – areas above the local water table, lawns – areas of relatively level surface, and hollows – areas lower than the local water table. In fen ecosystems, pools (flarks) can also occur. On bog hummocks, *Sphagnum*-dominated patches (*Sphagnum*-hummocks) alternate with patches either dominated by lichens or ericaceous shrubs and a few bryophytes. In bog hollows, lawns with *Sphagnum* mosses dominating the bottom layer alternate with bare hollows (mud-bottoms), the wettest and periodically flooded parts, with much exposed peat. This level of subdivision is useful for predictions of biogeochemical and hydrological cycles, especially C dynamics. Some of the more common wetland ecological types and associated characteristic vegetation are shown in Table 3.

Canada has the greatest area of wetlands in the world, estimated to cover between 13 and 17% of the total land area. In addition to covering a vast area, wetlands contain greater than 5.07×10^{17} g of peat Tarnocai 1984) and store about 60% of all organic C in Canada (Forestry Canada 1992). Canadian peatlands sequester an estimated 0.025 to 0.037 Gt C yr^{-1} (Roulet 2000). The second largest contiguous peatland in the Northern Hemisphere is in Canada (Hudson Bay Lowlands) and covers part of northern Ontario (Gorham 1991). The Hudson Bay Lowlands region is flat and the mineral subsurface consists of highly impermeable marine silts and clays (and other deposits), which favour waterlogging (Riley 1994). Peatlands represent Canada's most important biological C pool and C fluxes between peatlands and the atmosphere may significantly affect global C cycles. However, C flux data for boreal peatlands in Canada are limited to a few selected sites (Moore and Knowles 1990; Gorham 1991; Bubier et al. 1993; 1995a,b, 1998, 1999; Bubier 1995; (Mossavi et al. 1996; Lafleur et al. 1997, 2001, 2003; Moosavi and Crill 1997; Suyker et al. 1997; Bellisario and Moore 1998; Frolking et al. 1998; Schreader et al. 1998; Joiner et al. 1999; Griffis et al. 2000a,b; Moore et al. 2002) and as such, knowledge of the contribution of Canadian wetlands to global C cycles is limited.

Boreal peatlands in Ontario

Total wetland area in Ontario is 312,780 km^2, of which about 93% is peatland (Tarnocai et al. 2000). This amounts to about 30% of the total wetland area in Canada. In Ontario, wetlands represent 31% and peatlands 29% of the province's total land area. The wetland distribution for Ontario is shown in Figure 6.

Conifer swamp, which is the dominant wetland type in northern Ontario, accounts for 43% of the total peatland area in northwestern Ontario (Riley and Michaud 1987) compared to 58% in northeastern Ontario (Riley 1994) (Table 4). The difference in peatland types across Ontario is also evident for fens, with 19% of the peatland area in northwestern Ontario occurring as fens (treed or open), compared to only 6% in northeastern Ontario.

Average peat depths are rather consistent across northern Ontario (Table 5). Thicket (i.e., alder) and conifer swamps, however, tend to have lower peat depths compared to bogs and fens (Table 5). Total volume of peat stored in northeastern Ontario peatlands is about 60% higher than that stored in northwestern Ontario (Table 6). Similar to peatland area, most of the peat volume is stored in conifer swamps in both northeastern and northwestern Ontario. Fens contain about 23% of the peat in northwestern Ontario, but only about 10% of that in northeastern Ontario. Open bogs contain 30 to 35% of the peat in both areas. Treed bogs contain about 72% of the peat in bog ecosystems in northeastern Ontario, whereas peat is relatively evenly distributed between open and treed bogs in the northwest. Differences in conifer swamp and fen areas between northeastern and northwestern Ontario will result in different C cycling and C fluxes at the peatland surface/atmosphere interface. Climate change will also affect C cycles differently in these areas.

Table 2. Vegetation characteristics of boreal fens and bogs (from Zoltai et al. 1988).

Peatland Type	Overstory layer	Shrub layer	Herb layer	Moss layer
Domed bogs	*Picea mariana* *Larix laricina*	*Chamaedaphne calyculata* *Ledum groenlandicum* *Kalmia polifolia* *Vaccinium vitis-idaea* *Vaccinium oxycoccus*	*Cornus canadensis* *Anemone quinquefolia* *Mitella nuda* *Trientalis borealis* *Coptis trifolia*	*Sphagnum neroreum* *Sphagnum fuscum* *Sphagnum girgensohnii* *Sphagnum magellanicum* *Pleurozium schreberi*
Northern Plateau bogs	*Picea mariana*	*Chamaedaphne calyculata* *Ledum groenlandicum* *Kalmia polifolia* *Vaccinium vitis-idaea* *Vaccinium oxycoccus* *Rubus chamaemorus*		*Sphagnum fuscum* *Pleurozium schreberi* *Hylocomium splendens*
Flat bogs	*Picea mariana*	*Chamaedaphne calyculata* *Ledum groenlandicum* *Kalmia polifolia* *Rubus chamaemorus* *Vaccinium vitis-idaea* *Vaccinium oxycoccus*	*Smilacina trifolia* *Oxycoccum quadripetalus* *Carex oligosperma* *Sarracenia purpurea* *Andromed glaucophylla*	*Sphagnum fuscum* *Sphagnum angustifolium* *Pleurozium schreberi* *Dicranum polysetum* *Dicranum undulatum*
Basin bogs	*Picea mariana*	*Chamaedaphne calyculata* *Ledum groenlandicum* *Kalmia polifolia* *Rubus chamaemorus*	*Eriophorum vaginatum* *Smilacian trifolia* *Oxycoccum quadripetalus*	*Sphagnum fuscum* *Sphagnum magellanicum* *Sphagnum fallax* *Pleurozium schreberi* *Hylocomium splendens* *Sphagnum angustifolium* *Polytricum strictum*
Horizontal Fens	*Larix laricina*	*Betula pumila* *Rhamnus alnifolia* *Myrica gale*	*Carex exilis* *Carex lasiocarpa* *Scripus caesptosus* *Menyanthes trifolia* *Scripus hudsonianus* *Equisetaum fluviatile* *Habenaria dilatata*	*Sphagnum teres* *Sphagnum warnstorfi* *Sphagnum fallax* *Campylium stellatum* *Drepanocladus revolvens* *Scorpidum scorpiodes*
Basin fens	*Larix laricina*	*Betula pumila*	*Carex aquatilis* *Carex lasiocarpa*	*Drepanocladus exannulatus* *Drepanocladus revolvens* *Campylium stellatum* *Calliergon giganteum* *Calliergon richardsonii* *Sphagnum angustifolium*

Table 2. Con't.

Peatland Type	Overstory layer	Shrub layer	Herb layer	Moss layer
Spring fens	*Larix laricina*	*Betula pumila* *Andromeda polifolia* *Salix pedicellaris*	*Carex interior* *Carex lasiocarpa* *Scripus caesptosus* *Eleocharis quinqueflora* *Muhlenbergia glomerata*	*Scorpidium scorpiodes* *Drepanocladun revolvens* *Campylium stellatum*
Northern Ribbed Fens	*Larix laricina* *Picea mariana*	*Betula pumila* *Salix candida* *Salix pedicellaris* *Andromeda polifolia* *Lonicera villosa* *Rhamnus alnifolia* *Ledum groenlandicum* *Chamaedaphne calyculata*	*Carex diandra* *Carex disperma* *Carex chordorrhiza* *Carex lasiocarpa* *Carex limosa* *Menyanthes trifolata*	*Scorpidium scorpiodes* *Drepanocladus revolvens* *Messia triquetra* *Cinclidium stygium* *Sphagnum fuscum* *Sphagnum megallancium* *Pleurozium schreberi* *Dicranum undulatum*
Feather Fens	*Larix laricina*	*Picea mariana* *Chamaedaphne calyculata*	*Carex* spp.	*Sphagnum warnsorfii*
Delta marshes		*Salix arbusculoides* *Salix glauca*	*Equisetum fluviatile* *Carex rostrata* *Carex aquatilis* *Carex lasiocarpa* *Carex chordorrhiza* *Scripus lacustris* *Typha latifolia* *Eleosharis palustris* *Zizania aquatica* *Phargmites australis* *Myiophyllum spicatum* *Nymphaea spp.* *Polygonum spp.* *Potamogeton spp.* *Dulichium arundinaceum* *Sparganium chlorocarpum* *Menyanthes trifolata*	*Sphagnum spp.*
Floodplain swamps	*Fraxinus nigra* *Picea glauca* *Betula papyrifera* *Ulmus americana* *Abies balsamea*	*Sambucus racemosa* *Prunus virginana* *Acer spricatum* *Ribes americanum* *Alnus rugosa* *Cornus stolonifera*	*Impatiens capensis* *Galium triflorum* *Rubus pubescens* *Trillium cernuum* *Caltha palustris* *Urtica gracilis*	*Climacium dendoides* *Plagiomnium cuspidatum* *Pylasiella polyantha*

Table 3. Dominant species by microtopographic group for wetland ecological types in Canada (from Bubier et al. 1998)

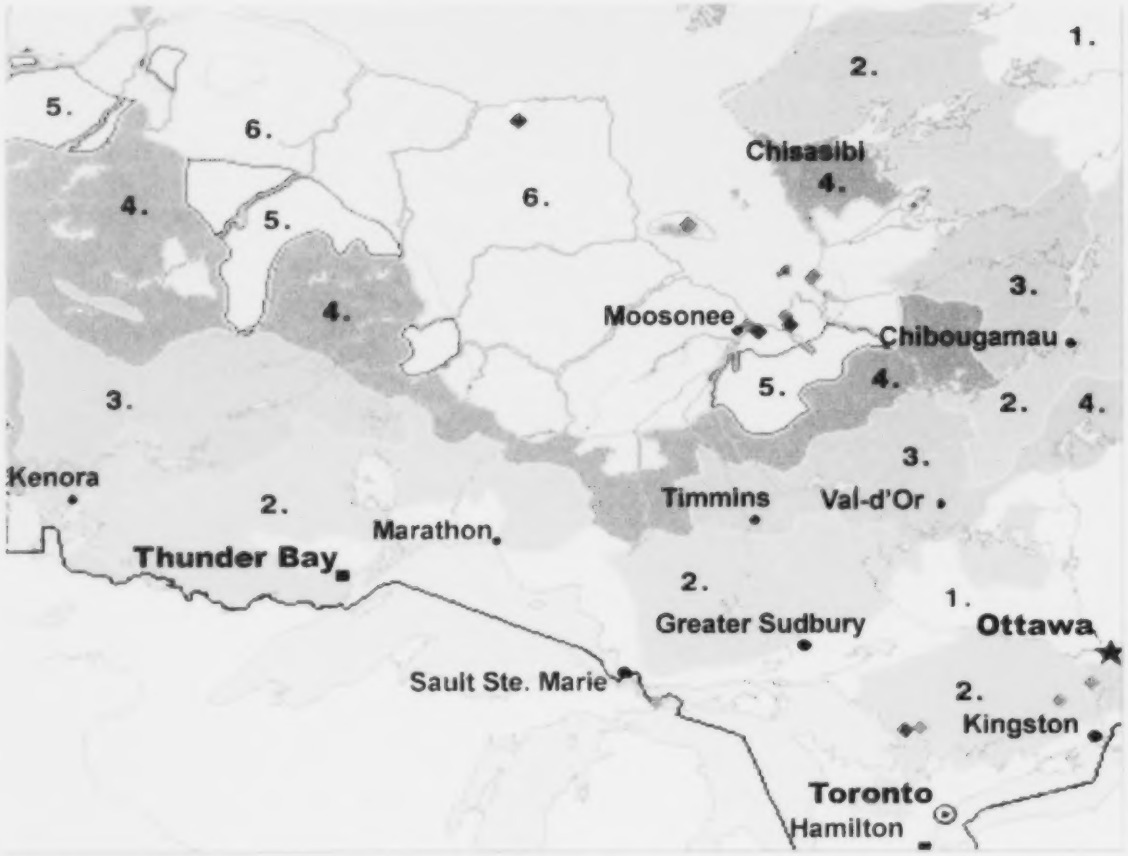
Ecological type	Hummock species	Hollow species	Lawn species
OgB	*Sphagnum majus* *Picea mariana* *Ledum groenlandicum*	*Sphagnum fuscum* *Carex limosa* *Rhynchospora alba*	*Sphagnum capillifolium* *Eriophorum spissum* *Carex pauciflora*
OlsB	*Sphagnum fuscum* *Ledum groenlandicum* *Chamaedaphne calyculata*	*Sphagnum angustifolium* *Carex oligosperma*	*Sphagnum fuscum* *Sphagnum capifolium* *Eriophorum spissum* *Pleurozium schreberi*
TlsB	*Sphagnum fuscum* *Chamaedaphne calyculata* *Picea mariana*	*Sphagnum angustifolium* *Smilacina trifolia* *Carex oligosperma* *Carex exilis*	*Sphagnum angustifolium* *Pleurozium schreberi* *Ledum groenlandicum*
CS	*Sphagnum fuscum* *Ledum groenlandicum* *Picea mariana*	*Sphagnum angustifolium* *Carex trisperma* *Carex pauciflora*	*Sphagnum capillifolium* *Chamaedaphne calyculata* *Ledum groenlandicum*
OlsF	*Sphagnum magellanicum* *Larix laricina* *Ledum groenlandicum* *Sphagnum fuscum* *Juniperus spp.*	*Warnstorfia exannulatus* *Sphagnum fallax* *Sphagnum warnstorfii* *Menyanthes trifoliata*	*Sphagnum angustifolium* *Sphagnum warnstorfii* *Sphagnum russowii* *Carex lasiocarpa* *Potentilla fruticosa* *Scripus hudsonianus*
TlsF	*Sphagnum magellanicum* *Picea mariana* *Larix laricina*	*Warnstorfia exannulatus* *Menyanthes trifoliata*	*Sphagnum angustifolium* *Betula pumila*
OgPF	*Sphagnum fuscum* *Polytrichum strictum* *Chamaedaphne calyculata*	*Sphagnum fallax* *Carex oligosperma* *Carex limosa*	*Sphagnum magellanicum* *Sphagnum capillifolium* *Betula pumila*
OlsPF	*Sphagnum fuscum* *Ledum groenlandicum* *Chamaedaphne calyculata*	*Sphagnum fallax* *Carex oligosperma* *Menyanthes trifoliata*	*Sphagnum capillifolium* *Kalmia polifolia*

[a] OgB = open, graminoid bog, OlsB = open, low shrub bog, TlsB = tall shrub bog, CS = conifer swamp, OlsF = Open, low shrub fen, TlsF = tall shrub fen, OgPF = open, graminoid poor fen, OlsPF = open, low shrub poor fen

Wetland Regions (1:7 500 000)

1. < 5%
2. 5% - 10%
3. 10% - 25%
4. 25% - 40%
5. 40% - 65%
6. > 65%

Figure 6. Proportion of area covered by wetland in northern Ontario (from Environment Canada, http://atlas.gc.ca/site/english/freshwater/distribution/wetlands/).



Wetland Regions (1:7 500 000)

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5. 40% - 65%
6. > 65%

Figure 6. Proportion of area covered by wetland in northern Ontario (from Environment Canada, http://atlas.gc.ca/site/english/freshwater/distribution/wetlands/).

Table 4. Percentage of area occurring as peatlands and total peatland area for northeastern and northwestern Ontario [adapted from Riley and Michaud (1987) and Riley (1994)].

Study area	Open bog	Treed bog	Open fen	Treed fen	Conifer swamp	Hardwood/ Mixedwood swamp	Thicket swamp	Marsh	Total peatland area ha	% of total area as peatland
					% total peatland area					
Northeastern Ontario[a]										
Hearst	1.3	8.1	4.4	6.3	58.0	0.2	16.9	4.9	338,889	21.2
Foleyet	1.1	11.7	1.6	5.4	74.7	0.4	3.2	2.0	292,420	17.8
Cochrane-Kapuskasing	8.8	23.2	2.1	1.2	53.2	-	9.2	2.3	528,795	33.1
Timmins-Kirkland Lake	8.2	19.6	0.4	1.5	50.6	-	14.9	2.2	321,290	15.3
New Liskeard	2.2	3.2	2.9	0.6	60.7	0.6	28.3	1.6	107,555	13.0
Total	5.2	15.8	2.3	3.5	58.1	0.2	12.2	2.7	1,588,949	20.5
Northwestern Ontario[b]										
Rainy River	13.0	12.2	7.6	9.1	19.6	5.2	26.7	6.5	116,112	26.2
Dryden-Lac Seul	4.5	25.4	3.4	7.4	41.8	<0.5	11.9	5.2	84,341	3.5
Sioux Lookout	6.6	9.1	9.9	7.5	50.6	-	13.5	2.8	95,096	5.9
Ignace	4.6	19.7	5.0	15.2	43.8	-	6.8	5.1	193,536	12.1
Armstrong	5.2	21.7	5.7	21.4	32.4	-	10.4	3.1	9,580	2.8
Longlac-Nakina	2.0	4.6	5.8	16.4	52.8	1.3	11.6	9.5	201,508	8.4
Total	5.5	13.4	6.2	12.6	42.9	1.3	13.1	5.1	700,173	8.0

[a] from Riley (1994) [b]from Riley and Michaud (1987)

Table 5. Average peat depth estimates (m) for northeastern and northwestern Ontario [adapted from Riley and Michaud (1987) and Riley (1994)].

Study area	Open bog	Treed bog	Open fen	Treed fen	Conifer swamp	Hardwood/ Mixedwood swamp	Thicket swamp	Marsh
Northeastern Ontario[a]								
Hearst	2.2	2.4	2.0	2.3	1.3	-	1.1	1.8
Foleyet	2.9	2.3	2.3	2.2	2.0	-	-	1.6
Cochrane-Kapuskasing	2.3	1.6	3.8	2.3	1.0	-	0.8	-
Timmins-Kirkland Lake	2.4	1.9	2.4	2.1	1.6	-	1.3	-
New Liskeard	4.3	3.4	1.9	1.5	1.9	1.3	1.9	-
Northwestern Ontario[b]								
Rainy River	3.6	4.0	2.6	2.8	3.2	-	2.0	1.3
Dryden-Lac Seul	2.0	1.9	1.9	1.7	2.5	-	0.9	2.5
Sioux Lookout	2.8	2.3	3.1	2.3	2.0	-	0.8	-
Ignace	2.4	2.4	2.2	2.6	1.8	-	2.0	3.4
Armstrong	2.7	2.5	2.0	2.1	-	-	-	-
Longlac-Nakina	2.8	2.9	2.4	2.1	0.8	-	-	-

[a]from Riley (1994) [b]from Riley and Michaud (1987)

Table 6 . Regional peat volume estimates for northeastern and northwestern Ontario [adapted from Riley and Michaud (1987) and Riley (1994)].

Study area	Open bog	Treed bog	Open fen	Treed fen	Conifer swamp	Hardwood/ Mixedwood swamp	Thicket swamp	Marsh	Total
Northeastern Ontario[a]				Volume (x 10^6 m^3)					
Hearst	99.0	628.6	329.3	446.1	2,554.2	5.6	628.1	167.1	4,858.0
Foleyet	100.2	750.1	96.4	397.7	3,058.2	12.0	110.9	57.0	4,564.5
Cochrane-Kapuskasing	1,021.6	2,084.8	384.4	152.6	2,249.6	-	389.8	123.9	6,406.7
Timmins-Kirkland Lake	607.8	1,260.8	61.4	219.5	2,112.4	-	576.0	69.9	4,907.8
New Liskeard	77.1	96.0	65.8	9.8	1,175.0	8.0	425.7	17.5	1,874.9
Total	1,905.7	4,820.3	937.3	1,225.7	11,149.4	25.6	2,130.5	432.4	22,612
Northwestern Ontario[b]									
Rainy River	498.8	553.0	256.1	317.5	113.9	60.0	434.3	106.4	2,340.0
Dryden-Lac Seul	124.4	557.6	71.7	124.6	528.3	4.0	100.0	43.9	1,554.8
Sioux Lookout	155.6	182.2	282.9	150.1	721.2	-	128.6	26.8	1,647.4
Ignace	238.0	987.6	223.5	615.7	1,268.8	2.0	131.6	97.6	3,564.8
Armstrong	13.0	49.9	12.7	49.2	46.5	-	10.0	3.0	184.3
Longlac-Nakina	1,104.9	270.7	316.4	692.7	1,595.1	25.3	234.6	111.1	4,350.8
Total	2,134.7	2,601.0	1,163.3	1,949.8	4,273.8	91.3	1,039.1	388.8	13,642

[a]from Riley (1994) [b]from Riley and Michaud (1987)

Carbon Cycling in Boreal Peatlands

Peatland net primary production and litter decomposition

Peatland ecosystems accumulate C and peat because annual inputs via NPP generally exceed annual losses through decomposition of litter and peat, with low decomposition rates relative to NPP leading to peat and C accumulation (Gorham 1991). Most of the NPP in peatlands is released to the soil as plant litter, subsequently entering the decomposition pathway (Clymo 1984). A range of NPP values have been reported for Canadian peatlands, with the tree-layer of non-permafrost forested peatlands ranging from 27.0 g m^{-2} yr^{-1} (Szumigalski 1995) to 1011 g m^{-2} yr^{-1} (Reiners 1972), shrub-layer ranging from 2.7 g m^{-2} yr^{-1} (Reiners 1972) to 730.0 g m^{-2} yr^{-1} (Tilton and Bernard 1975), and herbaceous layer ranging from 3.0 g m^{-2} yr^{-1} (Richardson et al. 1978) to 2297 g m^{-2} yr^{-1} (Van der Valk and Davis 1978). Campbell et al. (2000) summarized NPP data of peatlands in continental Canada and adjacent areas in the U.S.; the reader is referred to that report for more complete NPP values.

Litter quality is the main factor regulating its decomposition within a peatland and plants differ widely in quality and quantity of litter they produce (Johnson and Damman 1993; Hobbie 1996; Aerts et al. 1999, 2001). Decomposition and subsequent nutrient mineralization are, therefore, strongly determined by growth and decomposition characteristics of dominant plant species. *Sphagnum* decomposition rates are slower than vascular plants, but possible causes have not been well documented (Johnson and Damman 1993, Aerts et al. 1999). Recent evidence, however, suggests higher concentration of polyphenols in *Sphagnum* compared to sedges may account for different decomposition rates between those 2 plant groups (Williams et al. 1998, Yavitt et al. 2000). Slower decay in *Sphagnum*-dominated bogs compared to fens has also been reported in comparative peatland studies using standard substrates (e.g., cellulose strips) that remove the influence of litter quality (Farrish and Grigal 1988, Verhoeven et al. 1990).Thus, abiotic conditions of peatlands also contribute to litter decomposition,

with low pH and nutrient content of bogs often attributed to their slow rate of decomposition.

Litter decomposition in peatlands has been measured using various methods, with the most common approach being to apply litter decomposition bags to field incubations (Bartsch and Moore 1985, Thormann et al. 1999, Scheffer et al. 2001). Results are traditionally reported as percent mass loss with decomposition constants sometimes calculated, while laboratory incubations are reported as either percent mass loss or CO_2 production (Aerts et al. 1995). Decomposition of *Sphagnum* is generally similar within species regardless of location or peatland type (Table 7). However, *Carex* decomposition varies both by location and peatland type, with decomposition generally higher in European than Canadian peatlands. This may be related to higher atmospheric nitrogen (N) deposition rates in Europe than Canada, which can stimulate peatland litter decomposition (Aerts et al. 1995, 2001).

Roots are important to C cycling and sequestration in peatlands, where decomposition and exudation of organic C and N contribute significantly to soil C and nutrient turnover (Bernard and Fiala 1986; Backeus 1990; Hornibrook et al. 1997, 2000; Waldron et al. 1999; Chasar et al. 2000a). Roots of different sizes play different roles in C cycling. Fine roots are composed of relatively high-quality organic matter that have rapid turnover and exude easily degradable organic C and N at high rates (McLaughlin et al. 1996b). Those characteristics significantly affect soil microbial communities. Coarse roots, in contrast, are not easily degradable and are not major contributors to root exudation, although small pieces of organic matter may slough off coarse roots (Alexander 1977). Coarse roots do not stimulate microbial communities to the degree of fine roots, although they transport C to fine roots. Coarse roots are also important for belowground C storage. The contribution of roots to belowground C cycles in peatlands, however, has not been well studied. This is an important knowledge gap because 30 to 80% of plant primary production in peatland vegetation can be allocated to roots (Moore et al. 1998).

Verhoeven and Aerts (1992) reported that *Carex* root litter is a major source of organic matter to fens in the Netherlands. Moore et al. (2002) reported belowground biomass of 2400 g m^{-2}, of which 300 g m^{-2} was fine roots (< 2 mm diameter) for a bog hummock site and 1400 g m^{-2} with 450 g m^{-2} of fine roots in bog hollows at the Mer Bleue peatland complex near Ottawa, Ontario. This contrasts with aboveground biomass of 587 g m^{-2} for the bog. They also estimated root biomass as 1299 g m^{-2} for a poor-fen compared to aboveground biomass of 317 g m^{-2}. Thus, belowground biomass is 4- to 6-times greater than that for aboveground in poor-fens and bogs, respectively, at the Mer Bleue peatland. Finer and Laine (1998) reported fine root production rates between 101 and 268 g m^{-2} yr^{-1} for a drained forested peatland in Finland. Nadelhoffer et al. (2002) reported root production rates of 75 g m^{-2} yr^{-1} in a wet sedge tundra and 56 g m^{-2} yr^{-1} in moist tussock tundra in Alaska.

Increases in C allocation to root hairs (< 80 µm diameter) from 18% during spring to 55% during early fall has been reported for subarctic tundra in Sweden using radiocarbon (^{14}C) analysis (Olsrud and Christensen in press). They suggested that the high C allocation to a rapid turnover pool such as root hairs reduces C incorporation into woody tissue, increasing the overall C cycling rate and decreasing ecosystem storage. Furthermore, recently translocated ^{14}C to roots of *Carex aquatilis* and *Eriophorum angustifolium* was rapidly incorporated into CO_2, CH_4, and dissolved organic C (DOC) in Alaska (King and Reeburgh 2002). Moreover, winter CO_2 production in subarctic heath tundra in Sweden was derived predominantly from recently fixed plant C, while CO_2 derived from bulk soil organic matter was low (Grogan et al. 2001). The 3 studies cited above indicate the importance of recently fixed plant C to its cycling, especially during fall and winter, which are periods commonly ignored in peatland C studies.

Different root decomposition rates occur within the *Carex* genera in the Netherlands, where decomposition increased in the order of *Carex dundra* roots < *Carex lasiocarpa* roots < *Carex lasiocarpa* rhizomes (Scheffer et al. 2001). The high decomposition rates of rhizomes were related to their chemistry, where rhizome litter had the lowest lignin content and the highest nutrient contents. *Carex aquatilis* rhizomes had the highest percent mass loss (75%) in boreal fens in Alberta, followed by *C. aquatilis* leaves (54%), *Salix planifolia* leaves (48%), *S. planifolia* roots (29%) and *Sphagnum fuscum* (21%) after 2 years of decomposition (Thormann et al. 2001). They further reported that most of the sedge peat and C in the fen originated from *C. aquatilis* leaves followed by its rhizomes. Conversely, the majorityof *S. planifolia* peat came from roots, followed by its leaves. *Pinus sylvestris* roots in Finland decomposed at similar rates (~40% mass loss) over 2 years in both *Sphagnum*- and *Carex*-peat (Domisch et al. 2000). It needs to be emphasized that the results cited above are

Table 7. Litter decomposition in northern boreal peatlands.

Wetland type	Latitude (°N)	Litter type	Linear decay coefficient (k')	Mass loss ($g\ m^{-2}\ yr^{-1}$)	Mass loss (%) (1 year)	Exponential decay coefficient (k)	Location	Reference
Bogs	54	*Sphagnum fuscum*	0.14	22		0.15	Alberta	Thormann et al. 1999
	54	*Carex lasiocarpa*	-	-	55		Alberta	Szumigalski and Bayley 1996
	54	*Sphagnum fuscum*	-	-	0.1	-	Manitoba	Reader and Stewart 1972
	54	*Polytricum juniperium*	-	-	14	-	Manitoba	Reader and Stewart 1972
	54	*Aulacomnium palustre*	-	-	9	-	Manitoba	Reader and Stewart 1972
	54	*Ledum groenlandicum*	-	-	14	-	Manitoba	Reader and Stewart 1972
	54	*Kalmia polifolia*	-	-	36	-	Manitoba	Reader and Stewart 1972
	54	*Chamaedaphne calyculata*	-	-	30	-	Manitoba	Reader and Stewart 1972
	54	*Vaccinium vitis-idaea*	-	-	39	-	Manitoba	Reader and Stewart 1972
	54	*Oxycocucn quadripetalus*	-	-	7	-	Manitoba	Reader and Stewart 1972
	55	*Sphagnum capillifolium (hummock)*	-	-	49	-	Scotland	Balyea 1996
	55	*Sphagnum pappilosum (lawn)*	-	-	65	-	Scotland	Balyea 1996
	55	*Sphagnum cuspidatum (hollow)*	-	-	29	-	Scotland	Balyea 1996
Intermittently anoxic (hollow)	57	*Sphagum cuspidatum*	-	-	16.5	-	Sweden	Johnson and Damman 1991
Intermittently anoxic (hummock)	57	*Sphagum cuspidatum*	-	-	20.3		Sweden	Johnson and Damman 1991
Anoxic (hollow)	57	*Sphagum cuspidatum*	-	-	16.1		Sweden	Johnson and Damman 1991
Anoxic (hummock)	57	*Sphagum cuspidatum*	-	-	18.1		Sweden	Johnson and Damman 1991
Intermittently anoxic (hollow)	57	*Sphagnum fuscum*	-	-	9.4		Sweden	Johnson and Damman 1991
Intermittently anoxic (hummock)	57	*Sphagnum fuscum*	-	-	10.6		Sweden	Johnson and Damman 1991
Anoxic (hollow)	57	*Sphagnum fuscum*	-	-	9.1		Sweden	Johnson and Damman 1991
Anoxic (hummock)	57	*Sphagnum fuscum*	-	-	9.5		Sweden	Johnson and Damman 1991

Table 7. Con't.

Wetland type	Latitude (°N)	Litter type	Linear decay coefficient (k')	Mass loss ($g\ m^{-2}\ yr^{-1}$)	Mass loss (%) (1 year)	Exponential decay coefficient (k)	Location	Reference
Poor fen								
Oligotrophic	49	*Sphagnum fuscum*	0.14	-	15	-	Ontario	Rochefort et al. 1990
Oligotrophic	49	*Sphagnum magellanicum*	0.18	-	26	-	Ontario	Rochefort et al. 1990
Oligotrophic	49	*Spagnum angustifolium*	0.25	-	28	-	Ontario	Rochefort et al. 1990
Minerotrophic	49	*Sphagnum fuscum*	-	-	12	-	Ontario	Rochefort et al. 1990
Minerotrophic	49	*Sphagnum magellanicum*	-	-	16	-	Ontario	Rochefort et al. 1990
Minerotrophic	49	*Spagnum angustifolium*	-	-	30	-	Ontario	Rochefort et al. 1990
Poor fen	54	*Carex limosa*	0.18	-	15	0.20	Quebec	Bartsch and Moore 1985
	54	*Carex rosata*	0.20	-	15	0.23	Quebec	Bartsch and Moore 1985
	54	*Scripus cespitosus*	0.12	-	12	0.13	Quebec	Bartsch and Moore 1985
	54	*Betula glandulosa*	0.22	-	21	0.24	Quebec	Bartsch and Moore 1985
	54	*Salix pedicellaris*	0.14	-	15	0.15	Quebec	Bartsch and Moore 1985
	54	*Sphagnum lindergii*	0.11	-	10	0.12	Quebec	Bartsch and Moore 1985
	54	*Sphagnum teres/ Sphagnum angustifolium*	0.16	20	-	0.17	Alberta	Thormann et al. 1999
	54	*Carex spp.*	0.50	13	-	0.69	Alberta	Thormann et al. 1999
		Betula pumila	0.36	14	-	0.45	Alberta	Thormann et al. 1999
	52	*Carex diandra*	-	-	22	0.38	Netherlands	Scheffer et al. 2001
	52	*Carex lasicarpa*	-	-	16	0.48	Netherlands	Scheffer et al. 2001
	52	*Sphagnum papillosum*	-	-	14	0.04	Netherlands	Scheffer et al. 2001
	52	*Sphagnum squarrosum*	-	-	18	0.06	Netherlands	Scheffer et al. 2001
	52	*Carex diandra*	-	42	-	-	Netherlands	Verhoeven and Toth 1995
	52	*Spagnum fallax*	-	28	-	-	Netherlands	Verhoeven and Toth 1995
Intermediate fen	63	*Carex rostrata*	-	-	55	-	Sweden	Ohlson 1987
Moderate-rich fen	54	*Tomenthypnum nitens*	.022	31	-	0.25	Alberta	Thormann et al. 1999
	54	*Carex spp.*	0.58	15	-	0.87	Alberta	Thormann et al. 1999
	54	*Betula pumila*	0.37	9	-	0.46	Alberta	Thormann et al. 1999

Table 7. Con't.

Wetland type	Latitude (°N)	Litter type	Linear decay coefficient (k^{-1})	Mass loss ($g\ m^{-2}\ yr^{-1}$)	Mass loss (%) (1 year)	Exponential decay coefficient (k)	Location	Reference
	52	*Carex diandra*	-	-	18	0.37	Netherlands	Scheffer et al. 2001
	52	*Carex lasiocarpa*	-	-	14	0.40	Netherlands	Scheffer et al. 2001
	52	*Sphagnum papillosum*	-	-	9	0.04	Netherlands	Scheffer et al. 2001
	52	*Sphagnum squarrosum*	-	-	-	0.001	Netherlands	Scheffer et al. 2001
Rich fen	54	*Carex limosa*	0.17	-	15	0.18	Quebec	Bartsch and Moore 1985
	54	*Carex rostrata*	0.13	-	10	0.14	Quebec	Bartsch and Moore 1985
	54	*Carex aquatalis*	0.16	-	15	0.17	Quebec	Bartsch and Moore 1985
	54	*Carex chordorrhiza*	0.21	-	20	0.22	Quebec	Bartsch and Moore 1985
	54	*Scripus cespitosus*	0.12	-	12	0.13	Quebec	Bartsch and Moore 1985
	54	*Betula glandulosa*	0.20	-	20	0.22	Quebec	Bartsch and Moore 1985
	54	*Salix pedicellaris*	0.18	-	19	0.20	Quebec	Bartsch and Moore 1985
	54	*Carex diandra*	-	-	71	-	Netherlands	Verhoeven and Toth 1995
	54	*Sphagnum fallax*	-	-	40	-	Netherlands	Verhoeven and Toth 1995
Floating fen	52	*Carex diandra (leaves)*	-	77	35	-	Netherlands	Scheffer and Aerts 2000
	52	*Carex diandra (roots)*	-	98	15	-	Netherlands	Scheffer and Aerts 2000
Transitional fen/Extremely rich fen	54	*Carex limosa*	0.25	-	30	0.28	Quebec	Bartsch and Moore 1985
	54	*Carex rostrata*	0.14	-	11	0.23	Quebec	Bartsch and Moore 1985
	54	*Carex aquatalis*	0.27	-	30	0.31	Quebec	Bartsch and Moore 1985
	54	*Scripus cespitosus*	0.16	-	15	0.17	Quebec	Bartsch and Moore 1985
	54	*Betula glandulosa*	0.17	-	18	0.18	Quebec	Bartsch and Moore 1985
	54	*Salix pedicellaris*	-	-	20	-	Quebec	Bartsch and Moore 1985
	54	*Sphagnum liberbergii*	0.08	-	-	0.08	Quebec	Bartsch and Moore 1985
Lacustrine sedge fen	54	*Carex spp.*	0.31	49	-	0.37	Alberta	Thormann et al. 1999
Riverine sedge fen	54	*Carex spp.*	0.52	109	-	0.74	Alberta	Thormann et al. 1999
	54	*Salix planifolia (roots)*	-	-	23	-	Alberta	Thormann et al. 1999
	54	*Salix planifolia (leaves)*	-	-	51	-	Alberta	Thormann et al. 1999
	54	*Carex aquatilis (rhizomes)*	-	-	33	-	Alberta	Thormann et al. 1999
	54	*Carex aquatilis (leaves)*	-	-	52	-	Alberta	Thormann et al. 1999
Riverine marsh	54	*Carex spp.*	0.57	86	-	0.84	Alberta	Thormann et al. 1999
Lacustrine marsh	54	*Carex spp.*	0.62	206	-	0.97	Alberta	Thormann et al. 1999

short-term; < 1- to 2-year durations. Therefore, the long-term decomposition of peatland plant litter is not well known. However, most litter mass loss occurs during the first 1 to 2 years of decomposition with losses attributed to leaching and breakdown of low complex material (Aerts et al. 2001). Longer term decomposition rates are thought to be regulated by the lignin content of litter and its breakdown (Aerts et al. 1999).

Peat accumulation and carbon sequestration

The combination of limited oxygen (O_2) diffusion into saturated peat, inherent resistance to decomposition of some peatland vegetative tissues, and cool peat temperatures lead to the low decomposition rates in northern peatlands (Johnson and Damman 1993, Belyea 1996, Belyea and Warner 1996, Aerts et al. 2001). Although both NPP and decomposition rates are low in peatlands, peat accumulation varies tremendously. For instance, peat occurring below 20 cm in a bog in Sweden varied in age from 7 to 173 years and 10 to 175 years were required to accumulate 0.25 g C m^{-2} (Ohlson and Okland 1998). Decay rates within bogs also vary greatly, where CO_2 emissions can range from 0.26 to 0.92 mg CO_2 m^{-2} y^{-1} (Hogg et al. 1994).

One reason for variability in peat accumulation is that peatlands consist of 2 layers (Figure 7). One is a 10- to 50-cm deep aerobic layer, referred to as the acrotelm (Ingram 1978). This stratum has high hydraulic conductivity and relatively high organic matter decomposition rates. The second layer is a thicker anaerobic lower region, called the catotelm. It has low conductivity and organic matter decomposition rates that are only about 0.1% of that in the acrotelm (Belyea and Clymo 2001). Most biological activity and water movement is confined to the acrotelm.

When plants die, organic matter is added to the acrotelm, after which 90 to 97% of it is lost as gaseous CO_2 emission to the atmosphere through decomposition. Thus, only 3 to 10% of the organic matter is transferred to long-term C storage in the catotelm (Hogg 1992; Hogg et al. 1994; Malmer and Wallen 1996, 1999; Belyea and Clymo 2001). The C balance and peat accumulation rate in peatlands are, therefore, strongly influenced by organic matter decomposition within the acrotelm layer (Clymo et al. 1998). The annual net rate of peat accumulation equals the transfer of organic matter from the acrotelm to the catotelm, minus losses to very slow decay throughout the catotelm (Clymo 1984).

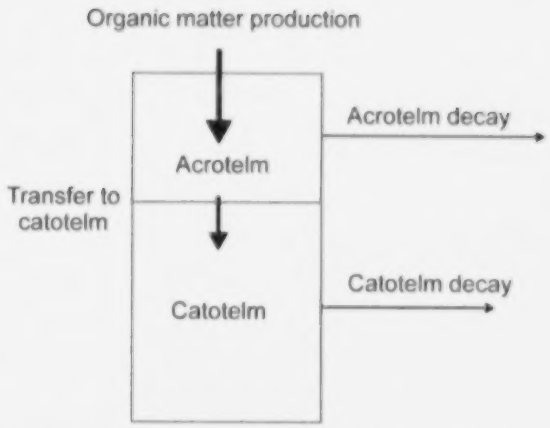

Figure 7. Schematic diagram of accumulation and decay of organic matter in peatlands. (from Belyea and Warner 1996).

The depth of the acrotelm is a function of regional and local physiography and climate, which determine peatland hydrology (Belyea and Clymo 2001), and vegetation communities, which influence evapotranspiration rates (Bubier et al. 2003a). While a portion of the organic matter is lost as CO_2 from the acrotelm via decomposition, the remaining organic matter is transported to the base of the acrotelm. At the same time, dead plant material is continuously added to the peat surface (Clymo 1984). These interacting processes reduce the integrity of the dead plant's main structural components and they collapse (Johnson and Damman 1993). Organic matter pore size decreases, bulk density increases, and capillary force of the organic matter increases in response to the collapse (Clymo 1984). This process is the main regulator of water table height in peatlands. When the water table is above its average height (i.e., after prolonged or heavy rain), most of the water flows rapidly through the large pore spaces in the acrotelm (Holden and Burt 2003). Water flow decreases when the water level falls to the acrotelm base where pore spaces of the collapsed organic matter are smaller. As hydrologic influx continues, the height of the water table rises to an average position just below the non-collapsed macroscopic organic material during successive years and peat accumulates (Johnson et al. 1990). Assuming constant climatic conditions, the boundary between the acrotelm and catotelm rises at the same rate as peat accumulates.

Local imbalances between peat formation and submergence affect acrotelm thickness (Belyea and Clymo 2001, Nungesser in press). When the ratio between water storage and specific water yield at the acrotelm/catotelm boundary equals the rate of peat

formation, the acrotelm thickens (Belyea and Clymo 2001). If the rate of submergence exceeds peat formation, then the water table rises relative to the vegetation surface. As a result, peat previously in the acrotelm becomes submerged and the acrotelm becomes thinner (Clymo 1984). If the rate of submergence is smaller than the rate of peat formation, only some of the newly formed peat is submerged and the acrotelm becomes thicker. The relationship between the rate of peat formation and acrotelm thickness determines the long-term dynamics of surface microtopography and rates of peat formation, with greatest peat formation occurring at an acrotelm thickness of about 10 cm (Belyea and Clymo 2001).

Because peatland hydrology plays a major role in the acrotelm/catotelm boundary, distinctions need to be made between fens and bogs. In bogs, minimal groundwater inputs (Siegel and Glaser. 1987, Vitt et al. 1994, Fraser et al. 2001) result in a highly fluctuating acrotelm, which, depending on precipitation inputs can be from the top of the peat surface to depths greater than a metre. In addition, evapotranspiration can further increase the depth of the acrotelm in bogs. Most frequently, however, the acrotelm in bogs is about 30 to 50 cm (Brown 1998, Nungesser in press). In fen systems, groundwater inflow results in a relatively consistent, thinner acrotelm depth, usually within 10 to 20 cm of the peat surface (approximate region of maximum peat formation (i.e., Belyea and Clymo 2001)).

The thin acrotelm of fens results in slower decomposition there compared to bogs (Bridgham et al. 1998). However, fens generally have more readily decomposable organic matter and deeper rooting of vegetation (can extend to depths greater than one metre below the surface of the peat) (Moore et al. 1998). In contrast, bogs have relatively low organic matter decomposability and relatively shallow rooting depths, often not exceeding 50 cm below the peat surface. Although organic matter in bogs is generally of lower quality for microorganisms, organic matter decomposition in the acrotelm of bogs is often more complete than in fens because of the thick aerobic layer of bogs (Nilsson and Bohlin 1993, Kuder and Kruge 2001). Thus, organic matter transferred to bog catotelms is more decomposed and more recalcitrant compared to fens (Johnson and Damman 1993), which have important implications to organic matter decomposition under climate change-induced warmer and drier conditions.

Carbon storage in Ontario's boreal peatlands

Carbon content, flux into peatlands, and transport from the acrotelm to the catotelm were estimated for Ontario's boreal peatlands using published information. An initial estimate of peatland C content was calculated using a weighted-mean bulk density of 152 g m^{-3} and weighted-mean peat C concentration of 51.8% for northeastern Ontario based on data from Riley (1994). For northwestern Ontario, a weighted-mean bulk density of 122 g m^{-3} and a weighted-mean C content of 51.5% were used for the estimate based on data from Riley and Michaud (1987) (Table 8). von Post humification classes 1 through 3 (Table 8) were used to calculate the weighted-means of dry bulk density and C concentration for the upper 50 cm of surface peat, while classes 4 through 8 were used to calculate weighted-mean bulk density and C concentration for peat occurring at depths greater than 50 cm. The proportion of peatland types reported by Riley (1994) and Riley and Michaud (1987) were used to represent peatland stratification across Ontario; i.e., northeastern Ontario was assumed to contain 69% of the peatlands and northwestern Ontario 31% of the total peatland area of 312,670 km^2 (Tarnocai et al. 2000). Those values were used in Equation 1 (Gorham 1991) to estimate total C content for each region. This equation gives a conservative estimate of peat C content in Ontario.

Carbon content=

(peatland area) x (peat depth) x (bulk density) x (peat carbon concentration)

Eq.1

Total peatland C storage in Ontario was estimated as 4.17×10^{16} g C m^{-2} or 41.7 Pg C. This represents 18 to 24% of C stored in Canadian peatlands and about 10% of C stored in northern peatlands worldwide. Peatland C content in northeastern and northwestern Ontario was estimated as 33.5 and 13.6 Pg C, respectively. Data from Riley (1994) and Riley and Michaud (1987) were used as the basis for distribution of peatland types in their respective regions. Figure 8 shows the C content for the different peatland types in the 2 regions. As with peatland area and peatland volume, conifer swamps contain most of the peatland C; 62% in northeastern Ontario and 54% in northwestern Ontario. Combined, conifer swamps and bogs account for approximately 90% of the peatland C storage in northeastern Ontario and 75% of the peatland C storage in northwestern Ontario.

An overall height accumulation rate of 0.5 mm yr^{-1} was used in Equation 2 to estimate the dry-mass C flux to Ontario peatlands (Gorham 1991).

Dry-matter carbon =

(peatland area) x (peat height accumulation) x (bulk density) x (peat carbon concentration)

Eq. 2

On an area basis, total C flux into northeastern Ontario peatlands is 8.85 x 10^{12} g C m^{-2} (8.85 Tg C m^{-2}), while C flux into northwestern Ontario peatlands is 2.76 x 10^{12} g C m^{-2} (2.76 Tg C m^{-2}). On an area basis, this amounts to 39 g C m^{-2} yr^{-1} for northeastern Ontario and 31 g C m^{-2} yr^{-1} for northwestern Ontario. The northwestern Ontario C flux is similar to that reported for the Experimental Lakes Area (ELA) (20 to 30 g C m^{-2} yr^{-1}) (Kelly et al. 1997). The northeastern Ontario value is slightly higher than that calculated for northwestern Ontario, that reported by Kelly et al. (1997) for the ELA, and the 29 g C m^{-2} yr^{-1} calculated by Gorham (1991) for dry-matter C flux into boreal and subarctic peatlands. The difference is the result of using 152 g m^{-3} as an estimate for bulk density, whereas Gorham (1991) used a mean bulk density value of 112 g m^{-3}. Gorham derived that value from an extensive database on Canadian boreal and subarctic peatlands that included those reported by Riley (1994) for northeastern Ontario. The northeastern Ontario C flux estimate is within the range of C sequestration rates reported by Roulet (2000) for northern peatlands (8 to 61 g C m^{-2} yr^{-1}). It also falls within the range for C accumulation for fens in Alberta (7.2 to 182.5 g m^{-2} yr^{-1}) (Yu et al. 2003), but is higher than that reported (13.1 to 21.8 g C m^{-2} yr^{-1}) for the Upper Mackenzie Valley of the Northwest Territories (Robinson and Moore 1999).

Using Clymo's (1984) equation (Eq. 3), the amount of C transported from the aerobic to anaerobic layer for long-term C storage can be calculated as:

$$m = (p/a) \times (1 - e^{-at})$$

Eq. 3

where m = accumulated mass on an area basis at time t, p = the annual rate of dry mass addition to the anaerobic peat mass after aerobic decay, and a = the fraction of decomposition in the total mass of the anaerobic layer, which continues to release CO_2 and CH_4.

Gorham (1991) reported the following values based on ^{14}C work on peat cores throughout Canada: p = 80 g m^{-2} y^{-1} and a = 0.00014. Applying these values to data provided by Riley (1994) and Riley and Michaud (1987) and using the total peatland area (2.25 x 10^{11} m^2 for northeastern Ontario and 8.76 x 10^{10} m^2 for northwestern Ontario) gives values of 1.16 x 10^{13} g C yr^{-1} for peatlands in northeastern Ontario and 2.01 x 10^{12} for those in northwestern Ontario for C transfer from the aerobic to the anaerobic peat layer.

These estimates are preliminary because conifer swamps and shrub bogs in Ontario vary in terms of depth to the water table and chemical composition (Bubier et al. 1993). However, these provide initial estimates of C storage for Ontario's boreal peatlands that can be used to evaluate Ontario's peatland contribution to regional, national, and global C cycles. Because boreal peatlands in Ontario potentially store up to 25% and 10% of the peatland C in Canada and the Northern Hemisphere, respectively, they likely play an important role in both national and global C cycles that should not be overlooked in addressing C-based, policy-related topics.

Although coniferous peatlands account for most of the peatland area and C storage in Ontario, limited information about C cycles within those peatland types is available (Bubier et al. 1993, 1995b; Charman et al. 1994; Bubier 1995). Much remains to be learned about the C cycling in coniferous swamps (and within peatlands, in general) in Ontario. Research efforts especially need to focus on net ecosystem exchange (NEE) of CO_2 and how shifts in climate or anthropogenic disturbances may alter net CO_2 fluxes and their associated C sink/source functions. Other than using flux towers, acceptable methodologies for developing NEE rates of CO_2 for conifer swamps do not exist. Although static chambers are used in open or low shrub fens and bogs to measure NEE of CO_2, they do not work well for conifer swamps. While ideal for research purposes, flux towers are expensive and too complicated for practical use, thus alternative methods are needed. In addition, litter and peat decomposition rates, peat quality, and mechanisms of C cycling need to be refined. A more complete understanding of potential hydrologic and vegetative effects on C cycling, and their response to both natural and anthropogenic disturbances, is required.

Table 8. Peat characteristics of von Post humification values for northeastern and northwestern Ontario [adapted from Riley and Michaud (1987) and Riley (1994)].

Parameter	von Post value							
	H1	H2	H3	H4	H5	H6	H7	H8
Northeastern Ontario[a]								
Dry bulk density (g cm^{-3})	0.07	0.09	0.11	0.13	0.17	0.18	0.13	0.17
Total carbon (%)	48.7	48.7	50.2	51.4	50.7	48.5	52.7	47.0
Northwestern Ontario[b]								
Dry-bulk density (g cm^{-3})	0.11	0.10	0.10	0.12	0.12	0.13	0.14	0.12
Total carbon (%)	47.5	47.4	51.1	51.8	51.3	51.9	49.4	52.0

[a]from Riley (1994) [b]from Riley and Michaud (1987)

The Walley Creek site provided information on the hydrology and C dynamics of conifer swamps in northeastern Ontario in relation to forest management (Berry 1991; Berry and Jeglum 1991a, b; Bubier et al. 1993; Charman et al. 1994; Bubier 1995). The site is currently inactive and should be resurrected to improve our understanding of C cycling and budgets in conifer swamps and to elucidate the interaction of climate change and forest management on conifer swamp C dynamics. Data from the Walley Creek site could be used in conjunction with study sites at the Mer Bleue peatland complex near Ottawa, the ELA near Kenora, Ontario's Fluxnet site near Foleyet, and our riparian wetland study near White River to support research interpretations of Ontario's wetland contributions to C cycles. Furthermore, collaborations among wetland researchers in Ontario, Manitoba, Quebec, Minnesota, and Michigan are needed to fully integrate regional wetland C cycling dynamics. With the limited data available for conifer swamps in Ontario, an important knowledge gap exists in peatland C cycles and fluxes within the province. Combined, these knowledge gaps make it difficult to predict peatland C cycles and the effects of climate change and other disturbances on Ontario's C budgets and cycles.

Carbon cycling dynamics

Oxidation - reduction reactions

Decomposition in peatlands occurs through 3 different processes: aerobic respiration, anaerobic respiration, and fermentation. Aerobic respiration produces the greatest energy for microorganisms and organic matter decomposition is more complete than for anaerobic respiration or fermentation (Schlesinger 1991). Under aerobic conditions, microorganisms (both bacteria and fungi) use O_2 as their terminal electron acceptor, resulting in relatively complete organic matter breakdown to CO_2 (Alexander 1977, Schlesinger 1991). When the water table is low, O_2 diffuses relatively freely into the upper layers of peat to maintain oxygenated conditions and aerobic respiration (Schlesinger 1991). Once the water table rises, after precipitation or flooding (or other disturbance) events, a thermodynamic sequence in microbial organic matter decomposition occurs (Table 9; Figure 9). Oxygen is first depleted because the elevated water table restricts O_2 diffusion into peat to replenish O_2 used up in aerobic respiration. At this point, anaerobic conditions are created and bacterial decomposition becomes dominant or exclusive, where nitrate (NO_3) is preferentially used as a terminal electron acceptor (Schlesinger 1991). As the redox potential continues to decline, manganese (Mn^{4+}), iron (Fe^{3+}), SO_4^{2-}, and finally CO_2 are used as bacterial terminal electron acceptors (Table 9), with each process producing subsequently less energy for microorganisms involved in the transformations.

The thermodynamic sequence of organic matter decomposition in peatlands has been determined for bacteria under pure culture situations in laboratories and the sequences under field conditions are often not

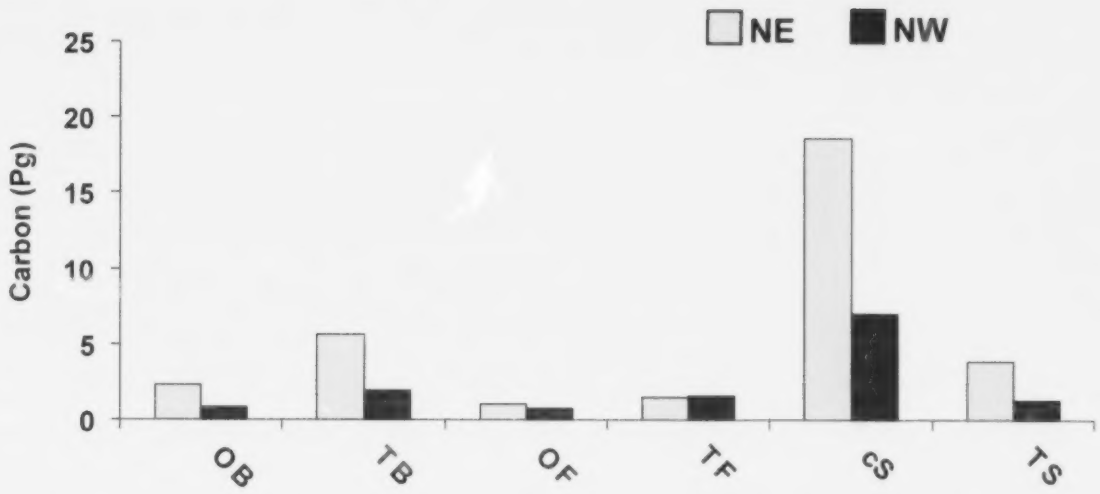

Figure 8. Estimated carbon content for boreal peatlands in Ontario. Carbon content was calculated from land area and peat depth of peatland types for northeastern (NE) Ontario (Riley 1994) and northwestern (NW) Ontario (Riley and Michaud (1987) (OB = open bog, TB= treed bog, OF= open fen, TF= treed fen, CS= conifer swamp, TS= thicket swamp).

straight forward. For example, it is generally reported that SO_4^{2-}-reduction (Schink 1997, Segers 1998) or denitrification (conversion of NO_3 to N_2) (Kluber and Conrad 1998, Scholten et al. 2002) processes inhibit methanogenic (CH_4-producing) processes. In terms of SO_4^{2-}-reduction, bacteria carrying out that process are more competitive than methanogens for substrates such as acetate and/or H_2. However, no inhibition of SO_4^{2-}-reduction on CH_4 production potential occurred at the Mer Bleue bog near Ottawa (Blodau and Moore 2003). In contrast, addition of SO_4^{2-} inhibited methanogenesis in a northern Minnesota peatland (Dise and Verry 2001). In the case of denitrification, it can inhibit methanogenesis through production and potential build-up of toxic concentrations of nitric oxides (NO, NO_2) (Kluber and Conrad, 1998, Scholten et al. 2002).

Acetate concentration may be the regulator of methanogenesis and when concentrations are high, methanogenesis can occur in the presence of SO_4^{2-}-reduction (Conrad 1999). However, when acetate concentrations are low, SO_4^{2-}-reducing bacteria will more effectively use acetate than methanogenic bacteria. Vile et al. (2003b) reported greater C flow through SO_4^{2-}-reduction than methanogenesis at high SO_4^{2-}-deposition compared to low SO_4^{2-}-deposition areas in Canada and Europe. However, the 2 processes combined accounted for less than 2% of the total anaerobic C flow regardless of SO_4^{2-}-deposition rate, suggesting anoxic C flow predominates through fermentation of peatland organic matter. Sulfate amendment at Bleak Bog, Alberta did not affect either SO_4^{2-}-reduction or methanogenesis (Vile et al. 2003a), again implying fermentation was the most important process in peatland anoxic C flow. Other research has also indicated fermentation is important to C flow in a number of anoxic systems, including peatlands. For instance, fermentation of organic matter to ethanol may be a dominant process in forested peatlands in New York, with most fermentation associated with tree roots in the acrotelm (Coles and Yavitt 2002). Organic acids or alcohols produced from organic matter fermentation may also diffuse to the acrotelm, where they are decomposed to CO_2 by aerobic microorganisms (Hines et al. 2001).

Peat may also serve as an intermediary in electron transfer during redox reactions in peatlands (Cervantes et al. 2000). In this process, humic and fulvic acids in peat serve as electron acceptors and donors for microbial anaerobic reduction of compounds such as SO_4^{2-}. This may accelerate anaerobic decomposition and C cycling compared to anaerobic processes utilizing SO_4^{2-} as the sole electron acceptor (Pires et al. 2003). However, very few studies have addressed fermentation or peat electron transfer in organic matter decomposition of peatlands. As such, the relative significance of these reactions in natural systems is unclear (Coates et al. 2002, Nurmi and Tratnyer 2002, Eschlbach et al. 2003, Stets et al. in press).

The vegetative community also influences which organic matter decomposition processes are dominant. For example, when N-fixing plants, such as species of the *Alnus* or *Myrica* genera, occur on a wetland, N is relatively continuously supplied. Nitrification (conversion of ammonium (NH_4^+) to nitrite (NO_2^-) to NO_3^-) reactions may occur at rates that provide a relatively stable supply of NO_3^- to fuel denitrification (Kierna et al. 2003). This may or may not inhibit other anaerobic processes, such as SO_4^{2-}-reduction and methanogenesis. No data were found in the literature to support or contradict this hypothesis. However, preliminary data that we have obtained from a histic-mineral soil forested wetland in Michigan suggests that nitrification, denitrification, and SO_4^{2-}-reduction can occur simultaneously in the presence of N-fixing plants (McLaughlin *unpublished data*). It is likely that nitrification occurs in the rhizosphere (region of soil under plant root influence) of N-fixing plants where O_2 is available and denitrification occurs in nearby anoxic zones (Armstrong et al. 2000). We are currently using microsensors for O_2, NO_3^-, SO_4^{2-}, H_2S, and redox potential within the rhizosphere of *Alnus* roots to more adequately define these processes.

The relationships among denitrification, SO_4^{2-}-reduction, methanogenesis, and redox reactions requires further biochemical, physiological, and molecular biological research to provide sufficient understanding of C cycling in Ontario's peatland resources. However, at this point, understanding how microbial processes affect C cycling and trace gas fluxes and how climate change may alter those processes is virtually unknown. In part, this lack of knowledge is due to a common assumption that microbial community structure has little relevance to large-scale biogeochemical models (Schimel and Gulledge 1998, Wirz in press). However, microbial communities are responsible for C turnover in peatlands and should be considered important in the development of optimal biogeochemical and C budget models that better predict the role of Ontario's peatlands in global C cycling.

Carbon flux partitioning

The partitioning of C transport into peatland surface/groundwater/surface water/atmosphere fluxes is an important uncertainty requiring research. Studies in arctic (Kling et al. 1991) and temperate (Riera et al. 1999) zones indicate that under saturated conditions, 20%, or more, of the soil respiration (CO_2 and CH_4) is transported into aquatic systems draining peatlands. Our research has identified that vegetation composition also influences the form of C at this interface (McLaughlin et al. *unpublished data*). When N-fixing plants are present, about 50% of the soil solution and groundwater C occurs as dissolved inorganic C (DIC). Without N-fixing plants, less than 10% of the C is DIC, with the remainder occurring as DOC. The elevated N concentration may be stimulating organic matter decomposition through denitrification and increased CO_2 production. We have also found that stream DIC levels are elevated in areas adjacent to N-fixing plants in our streamside riparian wetland study area. Our research has also provided preliminary evidence that DOC occurring under N-fixing vegetation is high quality and likely able to stimulate redox reactions other than denitrification.

The ecosystem importance of C chemical shifts between inorganic and organic compounds in relation to vegetation is not well documented. However, it is known that aquatic plants and autotrophic bacteria (Kjeldsen et al. 1997, Romani and Sabater 2000) can take up carbonates and free CO_2 for their energy generation, while DOC can serve as an energy source for heterotrophic microorganisms (Romani et al. 1998). This may result in internal C cycling and storage within surface waters draining peatland areas that retains C within the landscape (Palmer et al. 2001, Judd and Kling 2002). Portions of the gaseous C can also be emitted to the atmosphere from streams or lakes draining peatlands (Kling et al. 1991, Riera et al. 1999). It is therefore important to further identify the forms of C and its transport and cycling within aquatic ecosystems that drain peatlands. Ignoring these components of C cycling and transport may lead to significant underestimation of C fluxes and budgets, especially in the boreal forest region of Ontario where about 30% of the land surface is classified as peatland (Zoltai et al. 1988, Riley 1994).

Methane

Importance of peatland atmospheric methane loading

Methane has been the most studied component of peatland C cycles, mostly because global emission of CH_4 affects the oxidative capacity of the troposphere as well as influencing the radiative forcing in the earth's energy balance. Average CH_4 concentration in the Northern Hemisphere was reported as 1745 ppbv in 1998 (Prather et al. 2001), and the total burden is estimated to be 4,850 Tg (Monson and Holland 2001). Annual CH_4 emissions, estimated by analyzing air trapped in polar ice, were 180 Tg yr^{-1} during the 15th century and 200 Tg yr^{-1} at the beginning of the 18th

Table 9. Thermodynamic sequence for reduction of inorganic substances at pH 7.0

Reaction[a]	Redox potential (volts)
Disappearance of O_2	
$O_2 + 4H^+ \rightleftharpoons 4e^- 2H_2O$	0.816
Disappearance of NO_3^-	
$NO_3^- + 2H^+ + 2e^- \rightleftharpoons NO_2^- + H_2O$	0.421
Formation of Mn^{2+}	
$MnO_2 + 4H^+ + 2e^- \rightleftharpoons Mn^{2+} + 2H_2O$	0.396
Reduction of Fe^{3+}	
$Fe(OH)_3 + 3H^+ + e^- \rightleftharpoons Fe^{2+} + 3H_2O$	-0.182
Sulfate reduction	
$SO_4^{2-} + 10H^+ + 8e^- \rightleftharpoons H_2S + 4H_2O$	-0.215
Methane formation	
$CO_2 + 8H^+ + 8e^- \rightleftharpoons CH_4 + 2H_2O$	-0.244

century (IPCC 2001). Recent estimates of atmospheric CH_4 emissions are 300 Tg in 2000, potentially rising between 400 to 600 Tg by 2010 (IPCC 2001). Current concentrations are thus about twice that of the preindustrial era. During the last 2 decades, CH_4 concentration in the troposphere has increased at a rate of 1.1% per year (Prather et al. 2001).

Methane is approximately 32 times more effective in atmospheric radiative forcing than CO_2, and CH_4 remains in the atmosphere for 8 to 12 years (Bouwman 1990). However, CH_4 contributes about 2.6 times less than CO_2 to greenhouse warming, in part because of fairly rapid CH_4 conversion to CO_2 in the atmosphere (Monson and Holland 2001). Methane is also very chemically reactive and, therefore, involved in changes in the chemical composition of the atmosphere (Bouwman 1990). In particular, CH_4 reacts with hydroxyl radicals in the troposphere, reducing its oxidative power and ability to eliminate pollutants such as chloro-fluorocarbons (CFCs) leading to the production of other greenhouse gases [ozone (O_3), CO_2, carbon monoxide (CO)]. In the stratosphere, such reactions produce water vapour, which destroys the stratospheric O_3 layer, which is important because it acts as a natural barrier against detrimental solar radiation (Bouwman 1990).

Northern peatlands are a net source of atmospheric CH_4 (Bartlett and Harriss 1993, Cicerone and Oremland 1998). The postglacial development of northern peatlands has been estimated to have increased global CH_4 emissions by 10 to 30 Tg yr^{-1}, thus increasing atmospheric CH_4 concentrations. Between 6000 and 200 years ago, atmospheric CH_4 concentration rose from 0.60 to 0.75 ppbv, likely as a result of northern peatland development (Blunier et al. 1995). Methane emissions from peatlands north of 45° latitude are estimated as 38 Tg yr^{-1}, representing 34% of total CH_4 emission (Bartlettand Harriss 1993). The importance of northern peatlands in releasing CH_4 to the atmosphere is, however, currently uncertain. Crill (1996) divided the world's wetlands into 4 major latitudinal zones: tropical (0-20°), temperate (20-45°), boreal (45-65°), and arctic (>65°). He calculated that more than half of the annual CH_4 emission comes from boreal peatlands. In contrast, Bartlett and Harriss (1993) estimated that 60% of the CH_4 input to the atmosphere from wetlands was from tropical regions, while only 35% occurred from peatlands north of 45°.

The initial high estimates of the importance of boreal peatlands were based upon CH_4 emission rates observed in northern Minnesota peatlands (Crill et al. 1988, Dise 1993). Rates in Minnesota are 5 to 15 times higher than those reported for peatlands in the Hudson Bay Lowlands of Ontario (Klinger et al. 1994). The Hudson Bay data caused revision downward in the importance of northern peatlands in atmospheric loading of CH_4

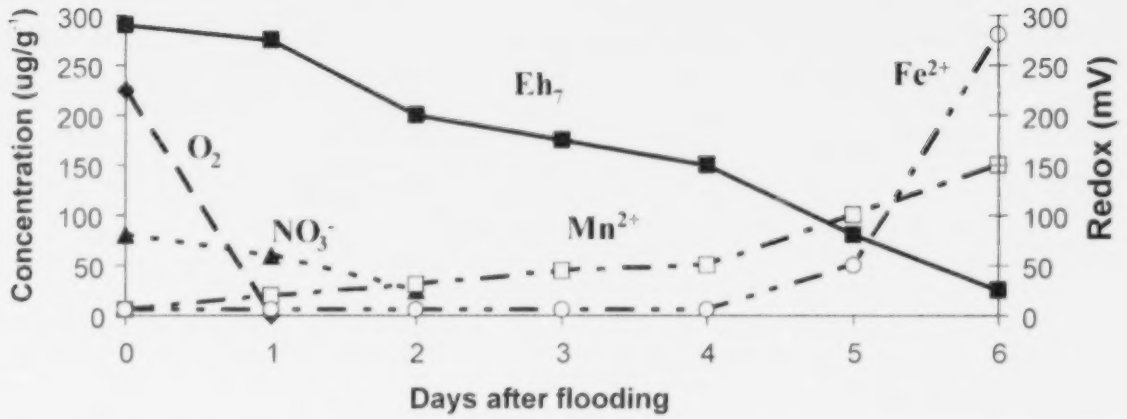

Figure 9. Changes in the chemical composition of waters overlaying a flooded soil as a function of time after flooding. Redox potential is expressed at pH7 (Eh7) (i.e., from Schlesinger 1991).

and focused attention to the tropics. More recent data (IGBP 1996), however, suggests that the Hudson Bay Lowlands may be more atypical of northern peatlands than the Minnesota peatlands. Therefore, there is an important need to refine the rates of CH_4 emissions to the atmosphere by boreal peatlands in the Northern Hemisphere.

Methane production in northern peatlands

Location and pathways of methane production

Methane production has received much attention because of its importance in anaerobic organic matter degradation and its potentially significant role in climate change and atmospheric chemistry (Roulet 1992, Amaral and Knowles 1994, Moore et al. 1994, Romanowicz et al. 1995, Roslev and King 1996, Shannon and White 1996, Chasar et al. 2000a, Christensen et al. 2003). Although the potential role of CH_4 in climate change is recognized, measuring rates of CH_4 production and consumption in peat soils is challenging. To advance the understanding of factors controlling CH_4 production and consumption in soils, assessment methodologies need to be improved (von Fischer and Hedin 2002).

Despite the methodological challenges, significant progress has been made in evaluating CH_4 production in northern peatlands. Methane production is the terminal process of organic C mineralization in peatlands and occurs when there is high input of labile organic matter in the absence of O_2 and alternative electron acceptors such as NO_3^-, Fe^{3+}, and SO_4^{2-} (Schlesinger 1991; Granberg et al. 1997, 2001). Methane is produced in the lower layers of the acrotelm and in the catotelm in virtually all types of peatlands, with most produced at the acrotelm/catotelm interface (Segers 1998, Le Mer and Roger 2001). Oxidation-reduction potential and organic matter availability are the major drivers of methanogenic bacteria (Hornibrook et al. 1997, Avery et al. 1999). The complete mineralization of organic matter in anaerobic environments occurs through methanogenic fermentation, which produces CH_4 and CO_2 based on the reaction:

$$C_6H_{12}O_6 \rightarrow 3\,CO_2 + 3\,CH_4$$

This transformation is accomplished through 4 populations of microorganisms that degrade complex molecules to simpler compounds including hydrolytic, fermentative, acetogenic, and methanogenic bacteria (Le Mer and Roger 2001). Methanogenic bacteria use only a few simple substrates: $H_2 + CO_2$, acetate, formate, methylated compounds, and primary and secondary alcohols (Segers 1998). The limited energy available in methanogenic conversion forces the microorganisms involved into a very efficient cooperation (Schink 1997). Mutual dependence of partner bacteria due to energy limitations can result in neither partner being able to operate in isolation; (i.e., syntrophic relationship); this synergenic cooperation is depicted in Figure 10.

In northern peatlands, acetate fermentation is commonly reported to account for 60 to 70% of the CH_4 emitted to the atmosphere, with the remainder

attributed to CO_2 reduction (Whiticar et al. 1986, Hornibrook et al. 1997, Avery et al. 1999). However, these percentages vary in response to organic matter quality, with more CH_4 released to the atmosphere from acetate fermentation of high quality organic matter, but more CH_4 released from CO_2 reduction when organic matter quality is low (Whiticar et al. 1986, Hornibrook et al. 1997). As such, the acetate pathway predominates in fens (Avery et al. 1999, Popp et al. 1999), whereas the CO_2-reduction pathway is often the dominant CH_4 production mechanism in bogs and conifer swamps (Yavitt et al. 2000, Duddleston et al. 2002).

Use of isotopes to study methane production

Stable isotope analyses are valuable tools for assessing the relative contributions of different CH_4 production pathways (Whiticar et al. 1986). The isotopic composition of ecosystem C (^{13}C and ^{12}C) provides a window into chemical reactions and physical and biological processes (Wang and Hsieh 2002). Isotopic analyses, therefore, provide powerful means to study the dynamics of C cycling in terrestrial (Ehleringer et al. 2000, Trumbore 2000, Wang and Hsieh 2002) and aquatic (Finlay 2001) ecosystems at various time scales. Isotopic analysis also provides constraints for evaluating the magnitude and timing of C responses to global environmental change and other ecosystem perturbations (Ehleringer et al. 2000, Trumbore 2000, Wang and Hsieh 2002).

By convention, stable C isotope ratios are expressed in delta notation (d) with units per thousand (‰) as:

$$d = ((R_{sample} / R_{standard}) - 1)) \times 1000‰ \quad \text{Eq. 4}$$

where R is the molar ratio of the heavy to light (^{13}C : ^{12}C) isotope of the sample or standard, generally Pee Dee Belemnite (PDB) (Trumbore 1999).

The $d^{13}C$ value of the atmosphere is enriched (-8‰) relative to plant biomass (-28‰) for Calvin Cycle plants (C_3 plants; which refers to the type of photosynthetic pathway used) because C_3 plant photosynthesis discriminates against the heavier ^{13}C isotope (Trumbore 1999) and the lighter ^{12}C isotope is preferentially used in plant photosynthesis in northern peatlands.

Stable isotope signatures of CH_4 relative to microbial respiratory production pathways were suggested as follows: acetate fermentation results in CH_4 relatively enriched in ^{13}C ($d^{13}C$ of -65 to -50‰). However, CO_2 reduction produces CH_4 with a $d^{13}C$ of -100 to -60‰ (Whiticar et al. 1986). In addition to C stable isotopes, hydrogen stable isotopes are also useful in delineating CH_4 production pathways where deuterium (dD) is depleted in the acetate pathway (dD = -250 to -531) relative to CO_2 reduction (dD = -172 to -250‰) (Whiticar et al. 1986). However, the use of stable isotopes has only recently been implemented in peatlands, and then only at a few peatland sites. Figure 11 presents possible peatland CH_4 production pathways based on the results of stable isotope studies.

Based on stable C isotope studies, researchers agree that CH_4 production in fens occurs via the acetate pathway in the upper peat layers, and shifts to CO_2 reduction in deeper peat (Avery et al. 1999; Popp et al. 1999; Chasar et al. 2000a, b). Although shifts in CH_4 production pathways may be common in fens, the depth at which this occurs varies. For example, the shift occurred at about 0.4-metre depth in a fen in Alberta (Popp et al. 1999); whereas, the acetate pathway was dominant to a depth of 1.0 metre for a fen in northern Minnesota before the shift to the CO_2-reduction pathway occurred (Chasar et al. 2000a). The predominant CH_4 production pathway in boreal, subarctic, and arctic bogs, as identified from stable isotope analysis, does appear to be CO_2 reduction, regardless of depth (Chasar et al. 2000a, b; Hines et al. 2001; Duddleston et al. 2002). However, both acetate fermentation and CO_2 reduction may operate in temperate bogs (Hornibrook et al. 1997, Avery et al. 1999).

Chasar et al. (2000b) reported that the rate of microbial respiration within a peat column of both fens and bogs was greater than peat decomposition rates in northern Minnesota. They found that the radiocarbon content of DOC ($D^{14}C$) at both bogs and fens was enriched relative to solid-phase peat by 150 to 300‰ (per mil for $D^{14}C$), which is consistent with the transport of recently produced DOC from photosynthesis downward into the peat column. Fen $D^{14}C$ for DIC and CH_4 closely tracked the $D^{14}C$ of pore water DOC at depth, indicating that recent plant production was the predominant substrate for microbial respiration. They also reported that upwelling groundwater contributed as much as 15% of the DIC to the bulk DIC pool at depth in the fen. The similarity of $D^{14}C$ values for DIC and CH_4 suggests that methanogens use DIC from the groundwater, as well as DIC produced in situ. Bog $D^{14}C$ values for pore water DIC and CH_4 differ by ≤ 15‰ at all depths and were depleted of ^{14}C relative to DOC by ~100‰, suggesting microbial use of a mixture of older and modern substrates. CO_2 reduction was reported as the primary pathway for methanogenesis at all depths in the bog.

Laboratory incubations

In addition to controlling substrate supply, plants affect the stable isotope distribution of CH_4 in emissions and porewater through plant-mediated transport mechanisms and root-associated aerobic CH_4 oxidation (Chaser et al. 2000a, b). *Carex* spp. and several other emergent aquatic plants use a passive-diffusive transport mechanism that results in mass-dependent fractionation of emitted CH_4 (Chanton et al. 1995), releasing CH_4 that is "lighter" (less ^{13}C) than the CH_4 dissolved in the shallow porewater. Chasar et al. (2000b) found that porewater CH_4 concentrations were consistently low to a depth of 1 metre in a *Carex*-dominated fen in Minnesota. In contrast, the CH_4 concentration of a *Sphagnum*-dominated bog approached maximum levels immediately below the water table. King et al. (1998) reported an inverse relationship between porewater CH_4 concentration and sedge root density in a fen in Alaska. Here removal of sedges from fens resulted in CH_4 emission reductions of 8- to 9-fold compared to controls where sedge vegetation was not removed. Similarly, Popp et al. (1999) reported that removal of sedge vegetation at a fen in Alberta almost completely inhibited CH_4 emission. This indicated that sedge roots provide O_2 for CH_4 oxidation in the rhizosphere and/or plant uptake of CH_4 from the rhizosphere and its transport within the plant from where it is emitted to the atmosphere. These studies provide strong evidence that sedge root density is critical in CH_4 cycling in fens. Verville et al. (1998) reported that not only are sedge roots important for CH_4 cycling, but so too is the moss layer. They removed the moss layer and found an increase in CH_4 emission, which was attributed to loss of CH_4 oxidation capacity within the moss layer.

Measuring potential CH_4 production rates of soil slurries or soil cores in laboratory incubations is another method of estimating relative CH_4 production in peatlands. However, as there is no standard procedure used, approaches vary among studies (Segers 1998). Nevertheless, general patterns can be deduced from the literature. Moore et al. (1994) reported a range of potential CH_4 production rates from peat samples in the Hudson Bay Lowlands of Ontario. Eighty-seven percent of the sites they investigated had potential rates below 0.5 mg CH_4 g^{-1} peat d^{-1} at 10- to 20-cm depths, which they defined as very low to low production rates. Sixty-seven percent of the sites produced CH_4 at rates less than 0.5 mg CH_4 g^{-1} peat d^{-1} at 20- to 30-cm depths. They also reported that other than in a coastal marsh and forested fen, no general pattern was apparent for CH_4 production by peatland type.

Romanowicz et al. (1995) also reported that potential CH_4 production rates did not differ between bogs and fens in northern Minnesota. Schimel (1995) found no difference between peatland vegetation types and CH_4 production rates at Toolik Lake, Alaska. In contrast, Bergman et al. (2000) reported that potential CH_4 production rates were higher in fens than bogs in Sweden. Updegraff et al. (1995) also reported that potential CH_4 production rates were lower in bogs than fens in Minnesota. Interestingly, the studies of Romanowicz et al. (1995) and Updegraff et al. (1995) were both conducted in northern Minnesota, but reported different CH_4 production rates and trends by peatland type. Updegraff et al. (1995) reported microbial community responses may be complicated by the thermal history of a site, which may explain the differences reported in Minnesota peatlands. Furthermore, methanogenic bacteria are highly sensitive to O_2 and, once exposed, their CH_4 production rates may not rebound (Coles and Yavitt 2002). Thus, lowering of the water table may reduce CH_4 production, even after the water table rises.

Dinel et al. (1988) suggested that preferential retention of CH_4 occurred in deep peat water at the Mer Bleue bog in Ontario. Blodau and Moore (2003) reported that CH_4 production rates at Mer Bleue were stratified by depth, with rates increasing from 0 to 25 nmol CH_4 cm^{-3} d^{-1} in the surface peat to 22 to 44 nmol CH_4 cm^{-3} d^{-1} at 24 to 30 cm. At 42 cm, rates were near 0 nmol CH_4 cm^{-3} d^{-1}. Blodau and Moore (2003) also found low correlation between porewater CH_4 concentration and sedge (*Eriophorum*) roots, which contrasts with results from other peatland studies (e.g., King et al. 1998, Popp et al. 1999, Chasar et al. 2000b). However, root densities of *Eriophorum* at the Mer Bleue bog were very low (Blodau and Moore 2003).

Brown (1998) found that potential CH_4 production rates for the acrotelm were more than 100 times the rate of the catotelm at Mer Bleue. She reported the acrotelm/catotelm boundary at Mer Bleue occurs at around 50 cm. Based on this, the increase in potential production rates reported by Blodau and Moore (2003) likely represented a gradient in CH_4 production from the top to the bottom of the acrotelm. Brown (1998) reported that at least 2 different populations of methanogens occurred at Mer Bleue bog, which is consistent with other peatlands (Sundh et al. 1997, Krumholtz et al. 1999, Dedysh et al. 2001). Recent research has used biochemical (phospholipid fatty acids (PLFA)) or molecular biological probes (rRNA, DNA) to further determine population structures of

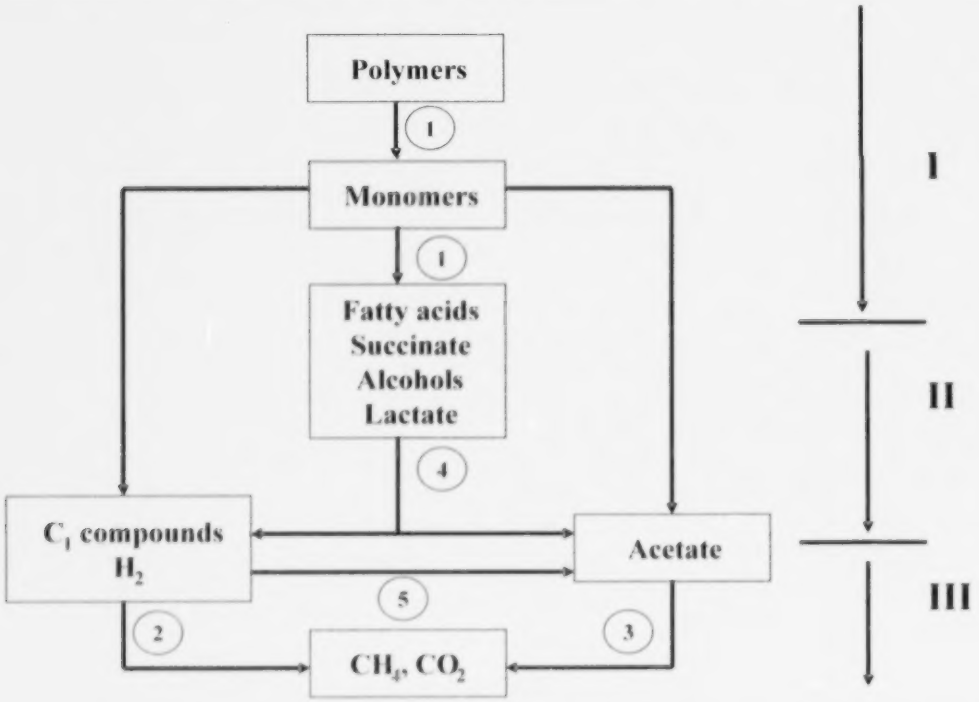

Figure 10. Carbon and electron flow through the various trophic groups of microorganisms involved in methanogenic degradation of complex organic matter in anoxic freshwater sediments. Groups of bacteria involved are: (1) primary fermenting bacteria, (2) hydrogen-oxidizing methanogens, (3) acetate-cleaving methanogens, (4) secondary-fermenting bacteria, (5) homoacetogenic bacteria. I, II, and III are steps in degradation (from Schink 1997).

methanogenic bacteria in northern peatlands (e.g., Sundh et al. 1997, Krumholtz et al. 1999, Wachinger et al. 2000, Dedysh et al. 2001, Pancost et al. 2002). Results from biochemical and molecular probes are providing valuable insight into total methanogenic populations, population counts for specific species, and relating specific species composition to C turnover in peat. These methods of methanogenic bacterial identification, however, are in early stages of development and have been used in few peatlands.

Methane emissions from northern peatlands

Transport mechanisms

Net CH_4 flux is the result of a complex set of interacting controls on production, transport, and consumption (von Fischer and Hedin 2002). As much as 80 to 90% of the CH_4 produced in the anaerobic zone may be oxidized before it reaches the atmosphere, with 30 to 80% being emitted as CO_2 after methanotrophic bacterial CH_4 oxidation. Those bacteria use the rest of the CH_4 for energy (Schink 1997, Le Mer and Roger 2001). Methanogenic and methanotrophic bacteria generally occur in close association with one another, within the region of the acrotelm/catotelm interface or within the rhizosphere soil. Methanogenic bacteria populate the anaerobic portion of the interface, while methanotrophic bacteria occur in the aerobic portion (Schink 1997; Conrad 1989, 1999).

Two mechanisms of CH_4 transport, ebullition and transport through aeranchyma of plants (particularly sedges), allow CH_4 produced in the peat profile to be emitted to the atmosphere through bypassing the aerobic acrotelm, and thus methanotrophic bacteria. Sedges can transport CH_4 internally and release it to the atmosphere (Whiting and Chanton 1993, Schimel 1995, Joabsson et al. 1999, Joabsson and Christensen 2001, Oquist and Svensson 2002). The vegetation that is common to bogs, however, does not function as a conduit for internal plant CH_4 transport and emission to the atmosphere. Methane oxidation in the rhizosphere can be quantitatively the most important location of oxidation in anoxic soils and varies according to the development stage of plants. However, few studies have been reported and those have mostly dealt with rice fields (Le Mer and Roger 2001). Understanding the interactions of

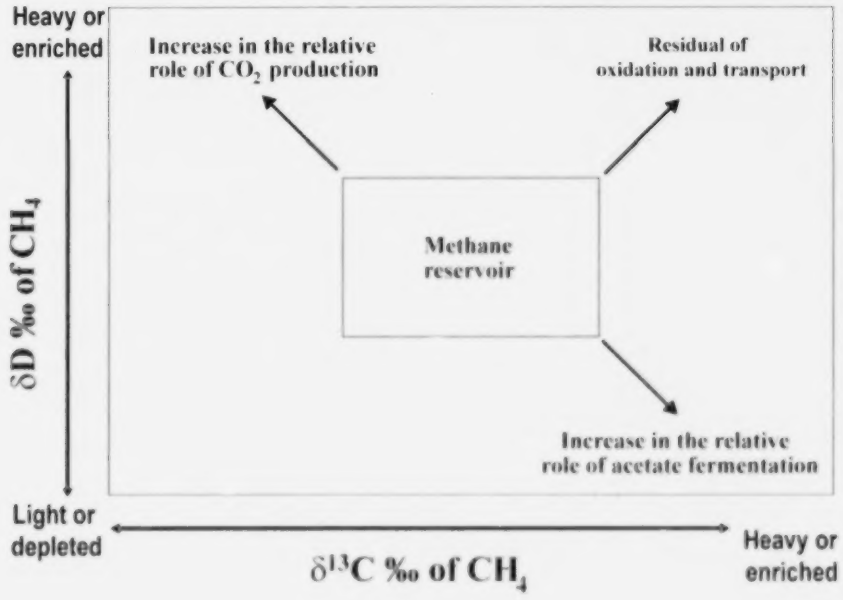
Heavy or enriched
Increase in the relative role of CO_2 production
Residual of oxidation and transport
Methane reservoir
Increase in the relative role of acetate fermentation
Light or depleted
Heavy or enriched
δD ‰ of CH_4
$\delta^{13}C$ ‰ of CH_4

***Figure 11.** Methane isotope effects revealed by $\delta^{13}C$ versus δD analytical methods (adapted from Popp et al. 1999).*

methanotrophs and methanogens at the acrotelm/catotelm interface and within the rhizosphere peat soil is critical for predicting CH_4 cycling in Ontario's peatlands and refining models of peatland contributions to global C cycles to reflect response to disturbance and climate change.

Northern Hemisphere regional methane emissions

Monitoring CH_4 emissions is important in the boreal zone (Segers 1998) because global climate models predict the region will experience increasing atmospheric CO_2 concentrations, temperatures, and altered precipitation patterns. However, in North America, CH_4 emissions have been measured in only a few areas: northern Minnesota (Harriss et al. 1985, Crill et al. 1988, Verma et al. 1992, Dise 1993); Schefferville, Quebec (Moore and Knowles 1987, 1990; Moore et al. 1990; Bubier et al. 1993); the Hudson Bay Lowlands (Klinger et al. 1994, Moore et al. 1994, Roulet et al. 1992, 1994); northeastern Ontario (Bubier et al. 1993, Bubier 1995); the Mer Bleue peatland near Ottawa (Frolking et al. 2002); central Alberta (Vitt et al. 1990); Manitoba (Bubier 1995, Bubier et al. 1995b); and Saskatchewan (Rask et al. 2002, Turetsky et al. 2002). Significant differences in CH_4 flux have been reported from these regions, making estimates of boreal peatland contributions to global C cycles uncertain.

CH_4 emission rates reported in the literature for boreal peatlands in North America are listed in Table 10, either as average daily or annual flux. These data were used, along with data reported for peatlands from arctic and boreal zones worldwide (Appendix I), to statistically analyze relationships among CH_4 emission, water table location, and peat temperature. Because the data were collected using different methodologies, and had non-normal distributions for CH_4 emissions and non-homogenous variances for CH_4, water table position, and peat temperature, non-parametric statistics were used. Because forested bogs and fens, treed bogs and fens, shrub bogs and fens were all categorized differently, 2 categories – fens and bogs – were used. These groupings were developed by lumping the various ecological groupings into either bogs or fens, respectively. Thus, for this analysis both bogs and fens are composed of different ecological types within their respective peatland type. Even though different methods were used to collect CH_4 flux data and various ecological types were lumped into the bog or fen categories, strong correlations were evident between CH_4 emission and water table position (Table 11) for both arctic and boreal regions, especially for fens. Methane emission was also significantly ($p < 0.05$) higher in boreal peatlands than in the arctic, which is likely related to temperature and water table differences between the biomes.

A major uncertainty in determining the contribution of northern peatlands to global CH_4 cycles has been discrepancies among the values for CH_4 emissions in the Northern Hemisphere, which indicate that Ontario has relatively low CH_4 emission rates (IGBP 1996). Data from boreal and subarctic peatlands published in the literature through February 2003 were summarized (Figure 12). Of the 11 locations shown in Figure 12, Ontario has one of the lowest CH_4 emission rates. Figure 13 compares CH_4 emission rates among peatland types for Ontario, Quebec, Manitoba, and Minnesota. Again, Ontario peatlands have the lowest CH_4 emissions rates for bogs and fens compared to Minnesota, Manitoba, and Quebec. A number of potential explanations exist for these trends. First, most Ontario peatlands are bogs and conifer swamps (Riley and Michaud 1987; Riley 1994; Tarnocai et al. 2000, 2002). Those 2 peatland types are known to have lower CH_4 emission rates than fens because the acrotelm is thicker and the vegetation is dominated by *Sphagnum* mosses, ericaceous shrubs, and black spruce rather than sedges as in peatlands at other locations. Thus, there is less internal plant transport of CH_4 in Ontario peatlands compared to other regions. Secondly, the organic matter in Ontario peatlands is of lower quality than that in peatlands occurring elsewhere (Yavitt et al. 2000). Finally, most fens in Ontario occur in the Hudson Bay Lowlands (Tarnocai et al. 2000), where cold temperatures inhibit microbial activity.

Organic matter quality and methane

Although much of the CH_4 efflux variation can be explained by environmental variables, some studies have shown that water table position and/or temperature explains only a small portion of the variation. Yavitt et al. (2000) reported that organic matter quality defined using holocellulose and Klason lignin fractions, was critical to CH_4 production and emission rates in a reciprocal transplant of peat samples from Ontario (ELA), Minnesota, and West Virginia. Microorganisms more easily decompose holocellulose than Klason lignin fractions (Williams et al. 1998). Yavitt et al. (2000) provided data that indicate limited methanogenesis in Ontario peatlands compared to those from Minnesota and West Virginia (Table 12). Work by Williams et al. (1998) supported the results of Yavitt et al. (2000). The former authors reported that peat from an ELA site had different chemistry in terms of Klason lignin and holocellulose compared to peatlands at more southerly locations (Minnesota, Ohio, New York). Moreover, Kuder and Kruge (2001) reported that peat at the Carling Lake Bog (Hudson Bay Lowlands of Ontario) has few cellulose compounds and more lignin-type compounds.

Surface peat from the ELA had about equal concentrations of both holocelluloses and Klason lignin, whereas holocellulose dominated surface peat from Minnesota and West Virginia (Yavitt et al. 2000). Subsurface peat from the ELA also had about equal concentrations of holocellulose and Klason lignin, but the concentration of Klason lignin increased and holocellulose decreased with depth in the peat at Minnesota and West Virginia. The larger proportion of Klason lignin in surface peat from the ELA than in surface peat from Minnesota and West Virginia is probably because the plant litter at ELA is relatively richer in lignin-type compounds, where greater proportions of *Sphagnum* and ericaceous plants occur at ELA and a higher density of sedges occur in the Minnesota peatland. Although *Sphagnum* mosses do not produce true lignin, they produce high concentrations of polyphenols (as do ericaceous plants), that are a component of traditional "lignin" fractions (Hattenschwiler and Vitousek 2000). Polyphenols inhibit organic matter decomposition, which may be an adaptation by plants to low nutrient sites (Cotrufo et al. 1998, Northup et al. 1998).

The highest rate of CH_4 production from surface peat incubated in Minnesota (Yavitt et al. 2000) was consistent with very high atmospheric CH_4 fluxes from northern Minnesota peatlands (Harriss et al. 1985, Verma et al. 1992, Shurpali et al. 1995, Shurpali and Verma 1998). In contrast, peat incubated at ELA produced less CH_4 (< 1 nmol kg^{-1} s^{-1}), regardless of peat origin. Further, the poor-quality organic matter at ELA probably resulted in a fewer methanogenic microorganisms, which would constrain CH_4 production from peat samples. These results also support the data shown in Figure 12, where CH_4 emission from Ontario peatlands is lower than that from Minnesota peatlands.

Methane emissions from Ontario's boreal peatlands

For Ontario, CH_4 emission rates for boreal peatlands were calculated using the mean fluxes obtained for fens, bogs, and conifer swamps from the literature (Figure 14). The data of Riley (1994) and Riley and Michaud (1987) were assumed to represent peatland distributions within northeastern and northwestern Ontario, respectively. A growing season of 150 days was assumed and a total

peatland area of 312,670 km^2 was used for area calculations for each peatland type. Based on these assumptions, total CH_4 emissions are 4.77 x 10^{11} g CH_4 m^{-2} yr^{-1} or 0.477 Tg m^{-2} yr^{-1}. Based on the estimate that boreal peatlands emit 10 to 30 x 10^{12} m^{-2} yr^{-1}, Ontario's peatlands contribute approximately 2 to 5% of the total CH_4 emitted by boreal peatlands in the Northern Hemisphere. Because it is well documented that peatlands in the boreal and arctic zones also emit CH_4 during the winter months and during spring snowmelt, which can account for 10 to 70% total emissions (Melloh and Crill 1996, Oechel et al. 1997, Winston et al. 1997, Fahnestock et al. 1998, Grogan and Chapin 1999, Lafleur et al. 2001, Aurela et al. 2002, Elberling and Brandt 2003), this is a conservative estimate. Bubier et al. (1993) reported that coniferous swamps in northeastern Ontario were negatively correlated with CH_4 flux; others have also deemed conifer swamps not important in atmospheric loading of CH_4 on a site basis (Moore et al. 1998, 2002). However, when Bubier et al. (1993) calculated habitat-weighted flux of CH_4 based on the aerial extent of each wetland type, conifer swamps accounted for 48% of the total regional CH_4 flux in northeastern Ontario. Using the distribution of peatland types, along with average CH_4 fluxes from a number of studies conducted in Ontario, this report calculates that conifer swamps contribute 45% to the northeastern Ontario region (similar to that calculated by Bubier et al. (1993)), but only 32% in northwestern Ontario. For the province as a whole, conifer swamps were calculated to contribute 42% to Ontario's peatland CH_4 flux. Charman et al. (1994) reported highest levels of CH_4 occurring at depths of 117 to 137 cm at the Walley Creek research site near Cochrane, Ontario. They related this to relatively slow decay of peat to a depth greater than 1 metre. In addition, levels were lower than peatlands in other regions (Bubier et al.1993, Bubier 1995, Romanowicz et al. 1995).

A more complete understanding of the relationship between peat chemistry and CH_4 production, oxidation, and emission is required for different peatland types (e.g., fens, bogs, conifer swamp) in Ontario to further our understanding of the role of organic matter quality in CH_4 production and subsequent emission rates. These data would be useful for refining models of CH_4 production and emissions in peatlands (Walter et al. 2001a, b). This is particularly important considering that Ontario contains about 10% of peatland C in Northern Hemisphere peatlands, but contributes only about 5% of total peatland CH_4 emissions in the Northern Hemisphere.

Carbon dioxide

Peatland importance to atmospheric CO_2

Carbon dioxide in peatland C cycles has not been studied as intensively as CH_4 because of the role of CH_4 in the oxidative capacity of the troposphere. However, CO_2 contributes more than other trace gases to greenhouse warming: about 2.6-fold more than CH_4 (Monson and Holland 2001). Furthermore, CH_4 is oxidized to CO_2 in the atmosphere relatively quickly (8-12 years), which is another reason CO_2 contributes more to warming than CH_4 (Bouwman 1990). Over the past 50 years, anthropogenic emissions of CO_2 have added an estimated total of 210 Pg of C to the atmosphere (Marland et al. 2001). During the same time period, atmospheric CO_2 concentration has increased by 55 ppmv from 310 ppmv in 1950 to 365 ppmv in 1998, which is equivalent to about 115 Pg C (Prentice et al. 2001). Predictions are that the amount of CO_2 emitted to the atmosphere will double within the 21st century (McGuire et al. 2001, Prentice et al. 2001). This increased atmospheric CO_2 concentration is predicted to have both direct and indirect effects on ecosystem structure and function (Moore et al. 1998, McGuire et al. 2001).

Determining the contribution of peatlands to atmospheric CO_2 is a major challenge because peatland net sink/source relationships can vary, even within the same year. Changes in winter temperature and precipitation may also affect sink/source relationships (Alm et al. 1999a). For instance, early snowfall and thick snowpack could insulate the peat surface from freezing and promote early winter CO_2 release from peat, while both soil temperature and CO_2 losses would decrease as a result of late snowfall or thin snowpack (Moore et al. 1998, Lafleur et al. 2003, Nykanen et al. 2003). Research from Alaska indicates that arctic tundra has become a stronger C sink during summer months, but also a larger C source during winter months, which has resulted in an overall increase in annual atmospheric C contributions (Hobbie et al. 1998, Gould et al. 2003, Le Dizes et al. 2003, McGuire et al. 2003). A major challenge from a research and monitoring perspective is to identify and separate natural variability from climate-induced change in the sink/source functions of boreal peatlands.

Table 10. Methane flux measurements from North American boreal peatlands.

Peatland type	Latitude (°N)	Average flux ($mg\ m^{-2}\ d^{-1}$)	Annual flux ($g\ m^{-2}\ yr^{-1}$)	Measurement period	Location	Reference
Bogs						
Forested bog	45	5.8	-	May - October	Manitoba	Roulet et al. 1992
Forested bog	47	89	-	May - August	Minnesota	Crill et al. 1988
Forested bog	47	100	-	August	Minnesota	Harriss et al. 1985
Forested bog						
Hummock	47	21	3.5	Annual	Minnesota	Dise et al. 1993
Hollow	47	93	13.8	Annual	Minnesota	Dise et al. 1993
Treed bog	49	-	0.7	June - Sept.	Ontario	Bubier et al. 1993
Treed-low shrub bog						
Hummock	49	0.1 to 5.1	-	May - October	Ontario	Bubier 1995
Hollow	49	5.3 to 11.1	-	May - October	Ontario	Bubier 1995
Lawn	49	5.2	-	May - October	Ontario	Bubier 1995
Open bog	45	20.6	1.7	May - October	Ontario	Roulet et al. 1992
Open bog						
Without Pools	49	-	0.8		Ontario	Bubier et al. 1993
With pools	49	-	8.3		Ontario	Bubier et al. 1993
Open, low shrub bog						
Hummock	49	0.2 to 1.8	-	May - October	Ontario	Bubier 1995
Hollow	49	11.4 to 12.28	-	May - October	Ontario	Bubier 1995
Lawn	49		-	May - October	Ontario	Bubier 1995
Open, graminoid bog		3.2 to 30.3				
Lawn	49	30.3	-	May - October	Ontario	Bubier 1995
Carpet/Pool	49	156.2	-	May - October	Ontario	Bubier 1995
Carpet	55	86.8 to 96.9	-	May - Sept.	Manitoba	Bubier et al. 1995a
Hollow	55	55.4	-	May - Sept.	Manitoba	Bubier et al. 1995a
Open, graminoid bog, carpet	55	86.8	-	May - Sept.	Manitoba	Bubier et al. 1995a
Nonforested bog	47	306	-	August	Minnesota	Harriss et al. 1985
Nonforested bog	47	199	-	May - August	Minnesota	Crill et al. 1988
Nonforested bog	47	177	-	August	Minnesota	Verma et al. 1992
Nonforested bog	47	356	43.1	August	Minnesota	Dise et al. 1993
Nonforested bog	54-55	0	0	May - October	Alberta	Vitt et al. 1990

Table 10. Con't.

Peatland type	Latitude (°N)	Average flux ($mg\ m^{-2}\ d^{-1}$)	Annual flux ($g\ m^{-2}\ yr^{-1}$)	Measurement period	Location	Reference
Bogs Cont.						
Domed bog						
Centre	45	-	0.1	May - September (multi-year)	Quebec	Moore and Knowles 1990
Margin	45	-	0.1		Quebec	Moore and Knowles 1990
Swamps						
Conifer swamp	45	0.15 to 7.1	-	May - September (multi-year)	Ontario	Roulet et al. 1992
Conifer swamp						
Dry	49	-	0.4		Ontario	Bubier et al. 1993
Wet	49	-	5.2		Ontario	Bubier et al. 1993
Conifer swamp-rich						
Hummock	49	5.9	-	May - October	Ontario	Bubier 1995
Lawn	49	19.2	-	May - October	Ontario	Bubier 1995
Conifer swamp-poor						
Hummock	49	0.5	-	May - October	Ontario	Bubier 1995
Lawn	49	3.2	-	May - October	Ontario	Bubier 1995
Conifer swamp, pool	49	109.1	-	May - October	Ontario	Bubier 1995
Mixed hardwood swamp	45	0.25 to 1.2	-	May - October	Ontario	Roulet et al. (1992)
Thicket swamp	45	0.4 to 69.3	-	May - October	Ontario	Roulet et al. 1992
Fens						
Forested fen	47	85	-	August	Minnesota	Harriss et al. 1985
Forested fen	47	142	-	May - August	Minnesota	Crill et al. 1988
Forested rich fen	54-55	24	3.4	May - October	Alberta	Vitt et al. 1990
Forest/fen margin	55	28	-	June - September	Quebec	Moore et al. 1990
Treed fen	49	-	4.3		Ontario	Bubier et al. 1993
Treed, tall shrub fen, hummock	55	5.7	-	May - September	Manitoba	Bubier et al. 1995a
Treed, low shrub fen, hollow	55	16.3	-	May - September	Manitoba	Bubier et al. 1995a
Treed, low shrub fen						
Hummock	49	0.1 to 0.6	-	May - October	Ontario	Bubier 1995
Lawn	49	0.3 to 12.4	-	May - October	Ontario	Bubier 1995

Table 10. Con't.

Peatland type	Latitude (°N)	Average flux ($mg\ m^{-2}\ d^{-1}$)	Annual flux ($g\ m^{-2}\ yr^{-1}$)	Measurement period	Location	Reference
Fens Cont.						
Carpet/Pool	45	34.6	-	May - October	Ontario	Bubier 1995
Open fen						
Dry	49	-	0.03		Ontario	Bubier et al. 1993
Wet	49	-	4.1		Ontario	Bubier et al. 1993
Open, low shrub fen						
Hummock	49	3.8	-	May - October	Ontario	Bubier 1995
Carpet	49	61.1	-	May - October	Ontario	Bubier 1995
Open, low shrub poor fen						
Hummock	49	2.5 to 3.1	-	May - September	Manitoba	Bubier et al. 1995a
Carpet	49	61.1 to 72.6	-	May - September	Manitoba	Bubier et al. 1995a
Lawn	49	29.3	-	May - September	Manitoba	Bubier et al. 1995a
Open, low shrub fen						
Carpet	55	55.3	-	May - September	Manitoba	Bubier et al. 1995a
Hollow	55	60.5 to 76.8	-	May - September	Manitoba	Bubier et al. 1995a
Open, graminoid fen, lawn	49	32.6	-	May - October	Ontario	Bubier 1995
Open, graminoid fen, carpet	55	92.3 to 210.2	-	May - September	Manitoba	Bubier et al. 1995a
Open, graminoid poor fen, carpet	55	60.6 to 108.3	-	May - September	Manitoba	Bubier et al. 1995a
Nonforested fen	47	348	-	May - August	Minnesota	Crill et al. 1988
Nonforested fen	47	402	65.7	August	Minnesota	Harriss et al. 1985
Nonforested poor fen	54-55	1	0.1	May - October	Alberta	Vitt et al. 1990
Nonforested rich fen	54-55	65	9.5	May - October	Alberta	Vitt et al. 1990
	54-55	24	3.4	May - October	Alberta	Vitt et al. 1990
Nonforested rich fen	55	30.5	-	June - August	Quebec	Moore and Knowles 1987
Nonforested fen						
Nonforested fen						
Centre	55	72	-	June - August	Quebec	Moore et al. 1990
Margin	55	30	-	June - August	Quebec	Moore et al. 1990

Table 10. Con't.

Peatland type	Latitude (°N)	Average flux ($mg\ m^{-2}\ d^{-1}$)	Annual flux ($g\ m^{-2}\ yr^{-1}$)	Measurement period	Location	Reference
Fens Cont.						
Pools/Flooded	45	34.6	-	May - October	Ontario	Bubier 1995
Patterned nonforested fen	55	33	-	June - August	Quebec	Moore et al. 1990
Ridges	55	7.5	-	June - August	Quebec	Moore et al. 1990
Pools	55	48	-	June - August	Quebec	Moore et al. 1990
Horizontal rich fen	55	-	3	May - Sept (multi-year)	Quebec	Moore and Knowles 1990
Horizontal poor fen	55	-	9.8	May - Sept (multi-year)	Quebec	Moore and Knowles 1990
Ribbed fen						
Ridges	55	-	1.3	May - Sept (multi-year)	Quebec	Moore and Knowles 1990
Pools	55	-	4.5/9.9	May - Sept (multi-year)	Quebec	Moore and Knowles 1990
Meadows/Marshes						
Sedge meadow	47	644	-	August	Minnesota	Harriss et al. 1985
Sedge meadow	54-55	148	21.7	May - October	Alberta	Vitt et al. 1990
Marsh	45	0.5 to 1.2	-	May - October	Ontario	Roulet et al. 1992
Marsh	49	-	22.4		Ontario	Bubier et al. 1993

* significant at $p < 0.05$

Measures of CO_2 exchange in peatlands

Methods used to measure CO_2 exchange

In contrast to CH_4, where soil respiration mostly controls CH_4 cycling, both photosynthesis and soil respiration interact to determine CO_2 exchange between peatlands and the atmosphere. Carbon dioxide exchange between peatlands and the atmosphere is defined as NEE of CO_2 and NEE can be used as an indication of the C sink/source strength of a peatland (e.g., Shurpali et al. 1995; Silvola et al. 1996; Bubier et al. 1998, 1999, 2003a,b; Lafleur et al. 2001, 2003). The NEE of CO_2 can also be used to estimate the net ecosystem productivity (NEP), which provides and indication of the annual C balance of a peatland in the absence of disturbance, over a given time scale (Bubier et al. 1998, Trumbore et al. 1999). Three methods are commonly used to estimate peatland NEP: (1) calculating NEP by subtracting heterotrophic respiration (HR) from NPP using both site-specific measurements and estimates derived from the literature, (2) assessing radiocarbon data from cores to derive long-term NEP, and (3) measuring NEP directly, combined with a model to fill in for days with no data. The 3 methods show similar magnitudes and patterns of NEP variation, but differ in the effort required, the sources of error, and the timescale to which they apply (Trumbore et al. 1999). Used in combination, they allow estimation of parameters such as belowground production and the contribution of heterotrophic decomposition to total soil respiration (Trumbore et al. 1999).

Net ecosystem productivity is the difference between annual NPP and HR; or gross primary productivity (GPP), autotrophic respiration (AR) and HR:

$$NEP = NPP - HR = GPP - AR - HR \quad \text{Eq. 5}$$

Table 11. Kendall Tau correlation coefficients (and sample size) for CH_4 emission, water table position, and peat temperature at 5° or 10°C for the boreal and arctic regions.

Variable	Variable		
	Methane emission	Water table position	Temperature
Arctic bogs			
Methane emission	1.0 (15)	0.36* (12)	0.12 (14)
Water table position	0.36* (12)	1.0 (12)	0.08 (12)
Temperature	0.12 (146)	0.08 (97)	1.0 (146)
Arctic fens			
Methane emission	1.0 (47)	0.67* (31)	0.14 (33)
Water table position	0.67* (31)	1.0 (31)	0.13 (31)
Temperature	1.0 (33)	0.13 (31)	0.14 (33)
Boreal bogs			
Methane emission	1.0 (168)	0.37* (95)	0.05 (82)
Water table position	0.37* (95)	1.0 (95)	0.09 (58)
Temperature	0.05 (82)	0.09 (58)	1.0 (82)
Boreal fens			
Methane emission	1.0 (132)	0.42* (77)	0.23* (64)
Water table position	0.42* (77)	1.0 (77)	0.52* (39)
Temperature	0.23* (64)	0.52* (39)	1.0 (64)

* significant at $p < 0.05$

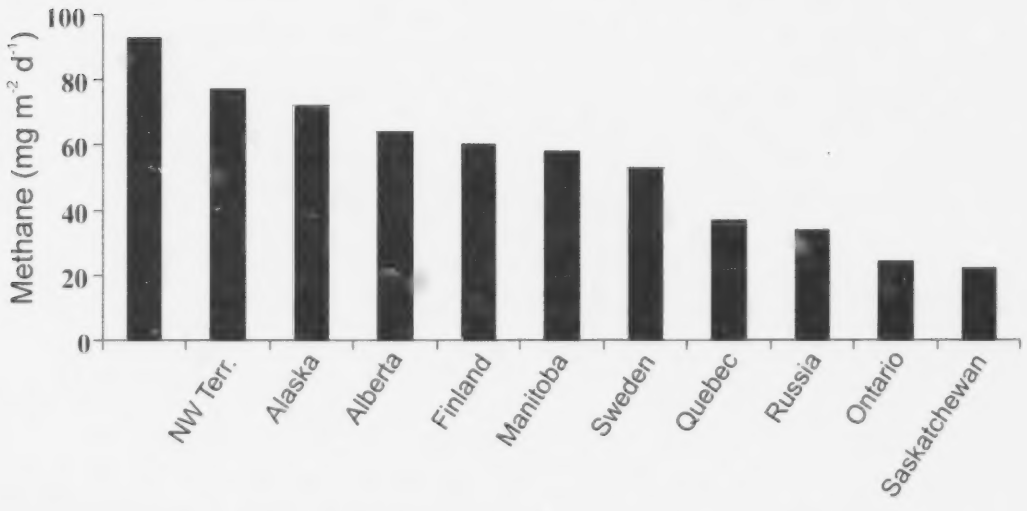

Figure 12. Mean methane emission rates from boreal and subarctic peatlands north of the 45th parallel.

Table 12. Yields of organic fractions of peat from 3 sites and 2 depths per site (from Yavitt et al. 2000).

Site	Holocellulose	Lignin
	mg g^{-1} dry peat	
Ontario		
5 cm	443	468
40 cm	451	478
Minnesota		
5 cm	792	275
40 cm	290	549
West Virginia		
5 cm	657	283
40 cm	197	715

Total soil respiration (TR) consists of HR plus belowground autotrophic respiration (BAR):

$$TR = HR + BAR \quad \text{Eq. 6}$$

NPP includes both above- (ANPP) and belowground (BNPP) components:

$$NPP = ANPP + BNPP \quad \text{Eq. 7}$$

Data can be obtained relatively easily for ANPP (measured by harvesting new plant increment after a 1-year period), instantaneous NEP (measured using clear chambers), GPP, and TR rates in equations (5), (6) and (7) (Trumbore et al. 1999). Other terms have proven difficult to determine directly, especially BNPP and HR. Annual production by roots is difficult to determine, particularly in fens where sedge roots can penetrate several metres into peat (Moore et al. 1998, 2002).

NEE measurements in North American peatlands

Measures of NEE of CO_2 in North American peatlands and tundra are shown in Table 13. Studies of bogs consistently indicate that they are net C sinks, with annual NEE estimates ranging from uptakes of 10 g C m^{-2} (Mer Bleue, Ontario) to 123 g C m^{-2} (northern Minnesota). In contrast to bogs, NEE estimates for fens in North America indicate that they are either net sinks or sources of atmospheric CO_2, with values ranging from an uptake of 88 g C m^{-2} (Prince Albert, Saskatchewan) to a net release of 145 g C m^{-2} (New Hampshire). However, NEE studies have been conducted on only a limited number of peatlands in North America and some studies report that interannual NEE values are highly variable for both fens and bogs (e.g., Griffis et al. 2000b, Lafleur et al. 2003).

The majority of the NEE literature has reported on mid-season observations from a limited number of sites. Furthermore, conflicting data for peatland C sink/source functions are often reported in the literature, with some studies showing peatlands functioning as net C sources (e.g., Lafleur et al. 1997, Aurela et al. 2002), while others report that peatlands are net C sinks (e.g., Griffis et al. 2000a; Lafleur et al. 2001, 2003; Roehm and Roulet 2003). In addition, the same peatland can be a net C source one year and a net C sink another year (e.g., Joiner et al. 1999, Griffis et al. 2000b). Also, some peatlands can alternate between a net sink and source of atmospheric C during different seasons of the same year (e.g., Suyker et al. 1997, Schreader et al. 1998, Griffis et al. 2000b). Moreover, different plant communities within the same peatland may be sinks or sources within the same year (Waddington and Roulet 1996). There are

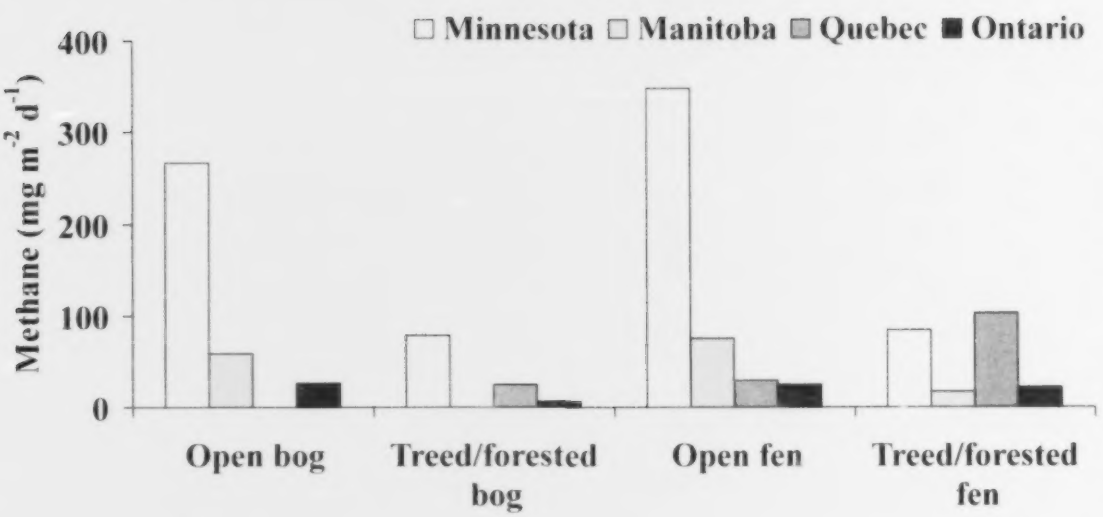

Figure 13. Comparison of mean methane emission to the atmosphere for different types of peatlands in Minnesota, Manitoba, Quebec, and Ontario.

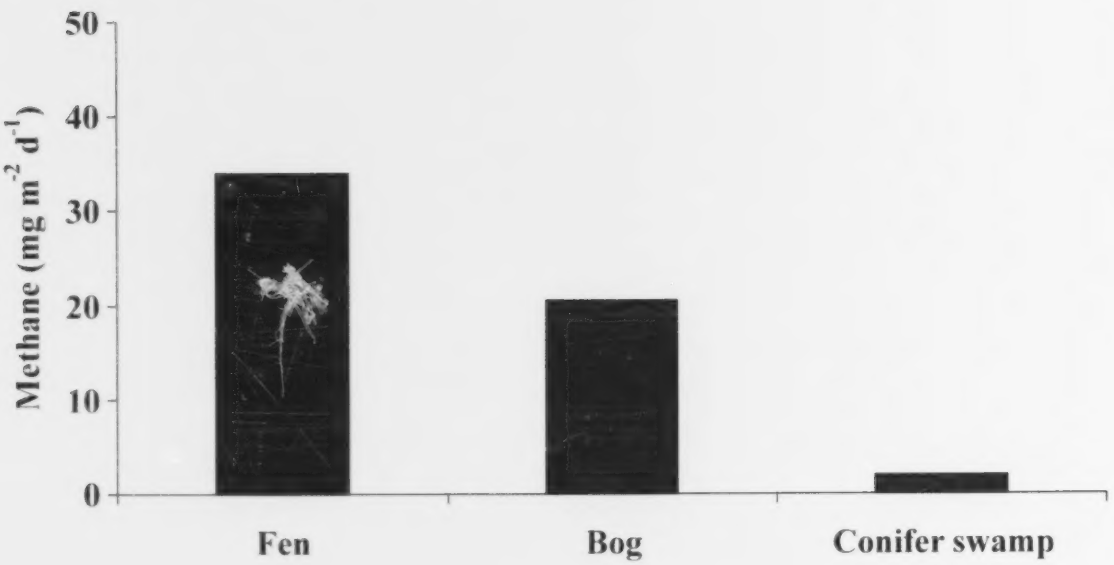

Figure 14. Mean methane flux for peatlands in Ontario (flux rates were calculated from data reported in Table 9 used in conjunction with total peatland area in Ontario and the distribution of each peatland type).

also significant differences in biogeochemical cycling of C in peatlands during different seasons (Melloh and Crill 1996; Oechel et al. 1997, 1998; Winston et al. 1997; Fahnestock et al. 1998; Grogan and Chapin 1999; Lafleur et al. 2001; Aurela et al. 2002; Elberling 2003; Elberling and Brandt 2003). Thus, there is limited ability to generalize C sink/source relationships for northern peatlands under current and projected climate scenarios. Longer-term tracking of NEE on peatland sites is critical to separate natural variability from that potentially caused by climate change.

Trends for the components of NEE of CO_2, photosynthesis and respiration, are different for different types of peatlands. For instance, Bubier et al. (1998) found that at a peatland complex near Churchill, Manitoba, maximum photosynthesis followed a sequence of bog < poor fen < intermediate fen < rich fen. However, NEP varied differently (Figure 15), where the poor and intermediate fens accumulated more CO_2, had higher NEP, and likely functioned as net CO_2 sinks over the season compared to the bog or rich fen. They also reported that bog and rich fen NEP may not be statistically different from zero. In contrast to the near zero CO_2 balance for the bog reported by Bubier et al. (1998), Lafleur et al. (2003) reported net uptake of CO_2 for the Mer Bleue bog in 3 of 4 years. The year of near zero NEE was dry, similar to results reported by Bubier et al. (1998) for Churchill, Manitoba.

Bubier et al. (2003b) reported vegetation differences in photosynthesis at a fen site in New Hampshire, where NEE values for *Chamadaephne calyculata* (leatherleaf) and *Alnus rugosa* (alder) dominated areas were higher than that of *Carex*, particularly during a dry year with a lower water table. The 2 shrubs and *Carex* also showed different trends in photosynthesis and ecosystem respiration in wet and dry years. For instance, leatherleaf and alder absorbed and released more CO_2 during a dry summer compared to a wetter summer. Maximum CO_2 uptake of *Carex* did not differ between wet and dry summers, but respiration rates were higher in the dry summer compared to the wet summer. The different seasonal and interannual patterns of CO_2 uptake among the 3 plant functional types reflect the differences in plant physiology and adaptations to moisture or drought stress.

Net ecosystem exchange of CO_2 varied across peatland types at Mer Bleue, likely due to differences in respiration (Bubier et al. 2003a). Wetter areas (i.e., poor fen and beaver pond margin) absorbed the most CO_2 and had the lowest respiratory loss during a dry summer. Communities dominated by ericaceous shrubs maintained similar photosynthetic rates in dry and wet summers, while sedge-dominated areas showed signs of early senescence and higher CO_2 release in the fall under drought conditions. Bubier et al. (2003a) reported that water table position had the most influence on respiration in the dry summer, whereas temperature had the most effect on respiration in the wet summer. Other studies have also reported the importance of precipitation or water table position on ecosystem respiration. For instance, Oechel et al. (1998) reported that water table drainage affected ecosystem respiration more than increased temperature in a wet-meadow sedge site in Alaska.

Joiner et al. (1999) reported that precipitation influenced net release of CO_2 from a fen near Thompson, Manitoba more than temperature. In a warmer year with more precipitation less net CO_2 was released than in a year with cooler temperature, but less precipitation, although both years had above-average overall temperatures. The year with less precipitation also had an earlier snowmelt, and warmer temperatures and drier conditions in the fall promoted soil respiration and CO_2 release when the vegetation was not photosynthesizing. This greater range of net CO_2 release resulted in the fen losing 30.8 g CO_2-C m^{-2} in the warm dry year, but gaining 91.6 g CO_2-C m^{-2} in the warm wet year. In contrast, Nykanen et al. (2003) reported that a palsa mire in Finland was a net C sink during both a dry and wet year, with average NEE values of 83.5 g CO_2-C m^{-2} uptake in the dry year and 106.9 g CO_2-C m^{-2} uptake in the wet year. These results are consistent with those reported by Lafleur et al. (2003), indicating a stable trend of net CO_2 uptake over a 4-year period at Mer Bleue in both wet and dry years. Griffis et al. (2000b) reported that at the fen site near Churchill, Manitoba, NEE varied over a 5-year study (Figure 16). The fen ranged from a net source of 76 g CO_2-C m^{-2} yr^{-1} to a sink of 235 g CO_2-C m^{-2} yr^{-1} and lost C nearly 3 times faster than its long-term average gain of about 11 g CO_2-C m^{-2} yr^{-1}. The results of Joiner et al. (1999) and Griffis et al. (2000b) suggest that climatic conditions before leaf-out and growth are critical to the sink/source strength of a peatland during the growing season.

Schreader et al. (1998) compared NEE values reported for 3 peatlands: Thompson, Manitoba (Lafleur et al. 1997); Churchill, Manitoba (Schreader et

Table 13. Landscape-scale estimates of net ecosystem exchange of carbon dioxide for North American boreal, subarctic, and arctic wetlands (negative values represent net uptake and positive values represent net release).

Location	Latitude (°N)	Year	Duration	Sum of NEE (g C m^{-2})	Daily NEE (g CO_2 m^{-2} d^{-1})	Reference
Bogs						
Mer Bleue, Ontario	45	1998-1999	May - June	-76	-1.9*	Lafleur et al. 2003
Mer Bleue, Ontario	45	1999-2000	May - June	-69	-1.6*	Lafleur et al. 2003
Mer Bleue, Ontario	45	2000-2001	May - June	-68	-1.5*	Lafleur et al. 2003
Mer Bleue, Ontario	45	2001-2002	May - June	-10	-0.5*	Lafleur et al. 2003
Quebec	45	1997	Feb. - Dec.	-76		Roehm and Roulet 2003
Lake Kinosheo, Ontario	51	1990	June - July	-56	-1.7	Neuman et al. 1994
Fens						
Barrington, New Hampshire	43	1994	March - Nov.	+145	+0.12	Carroll and Crill 1997
Prince Albert, Saskatchewan	43	1994	May - October	-88	-2.7	Suyker et al. 1997
Thompson, Manitoba	56	1994	May - Sept.	+31	+0.3	Lafleur et al. 1997
Thompson, Manitoba	56	1996	May - Sept.	-92	-1.0	Joiner et al. 1999
Churchill, Manitoba	58	1993	July - August	+30	+1.1	Burton et al. 1996
Churchill, Manitoba	58	1994	June - August	+21.9	+1.0	Schreader et al. 1998
Churchill, Manitoba	58	1996	June - August	-64.1	-3.1	Griffis et al. 2000b
Churchill, Manitoba	58	1999	June - August	-9.3	-0.5	Griffis et al. 2000b
Tundra						
Bethel, Alaska	61	1988	July - August	+9	+0.3	Fan et al. 1992
Alaska U-Pad, Sedge	70	1994	June - August	-66	-0.7	Vourlitis and Oechel 1997
Alaska U-Pad, Sedge	70	1995	May - Sept.	-48	-0.5	Vourlitis and Oechel 1997
Alaska 24-Mile, Sedge	70	1995	June - August	-101	-1.3	Vourlitis and Oechel 1997
Barrow, Alaska, wet tundra	71	1971	June - July	-69	-3.5	Coyne and Kelley 1975

* Summer-winter net ecosystem exchange

al. 1998); and Prince Albert, Saskatchewan (Suyker et al. 1997); by phenology stage during the relatively dry year of 1994 (Figure 17). The Thompson site lost the most CO_2 during the pre- and post-green periods. Fens at both the Thompson and Prince Albert sites increased net CO_2 uptake during the green period, whereas the NEE of CO_2 at the Churchill site was balanced. The green period lasted longer at the Thompson and Prince Albert sites than Churchill. Over the full measurement period, the Churchill site lost CO_2. In contrast, the Prince Albert site experienced only modest respiration losses in the pre- and post-green periods that were more than compensated for by substantial CO_2 uptake during the green period. Overall, in 1994 the more southerly sites (Thompson and Prince Albert) had longer growing seasons (green period) with much stronger photosynthetic CO_2 uptake.

Winter CO_2 flux

Carbon dioxide fluxes also vary according to microtopography and snowpack characteristics (Bubier et al. 1999, Griffis et al. 2000b, Aurela et al. 2002). Drier hummocks with no ice layers tend to emit CO_2, while inundated, ice-covered hollows or lawns have little or no CO_2 efflux until they thaw (Bubier et al. 1998, Nykanen et al. 2003, Lafleur et al. 2003). During the transition from snow cover to plant emergence, the different microforms generally do not melt and thaw at the same time (Shurpali et al. 1995, Oechel et al. 1997). Hummocks begin fixing CO_2 as soon as the moss layer is exposed, while lawns and hollows remain snow and/or ice covered and are atmospheric CO_2 sources. Hollows and lawns generally thaw days to weeks later than hummocks (Lafleur et al. 1997, Bubier et al. 1999, Griffis et al. 2000b). For instance, a hollow within 2 m of a hummock lagged 20 days in its onset of net CO_2 uptake. This lag corresponded with a similar lag in the warming of the peat above freezing at 5-cm depth (Bubier et al. 1998). These lag periods in combination with the proportion of hummocks, hollows, and lawns affect peatland atmospheric CO_2 sink/source relationships. The spatial variability in microtopography requires that peatland landscape-level C dynamic studies include small-scale measurements of microtopographic influences on C dynamics and appropriate landscape scaling (Bubier et al. 1997, 1999).

Lafleur et al. (2003) reported on the importance of winter CO_2 fluxes to the annual NEE of CO_2 at the Mer Bleue bog over a 4-year period. They reported a small but persistent winter CO_2 flux in all years (Figure 18) and suggested that snow cover through its effect on peat temperature influences decomposition and CO_2 exchange. Lowest total CO_2 loss and mean daily flux occurred in a winter with discontinuous snow cover, when mean January temperature in the hummocks cooled to -5°C at 5 cm – at least 3°C colder than in any of the other winters monitored. During the other winters, a continuous snowpack was established early in the winter and persisted until the main melt occurred in late March or early April. As a result, soil temperatures were considerably warmer, averaging only -1° to -2°C in the upper portion of the hummocks and near 0°C at 20 cm deep. Mean daily CO_2 fluxes were statistically similar during the 3 snowy winters. Other results across the Northern Hemisphere have also shown the importance of winter CO_2 release to annual peatland C budgets (Vourlitis and Oechel 1997, Panikov and Dedysh 2000, Heikkinen et al. 2002, Nykanen et al. 2003). Based on these results, not including winter CO_2 fluxes in calculations will overestimate the CO_2 sink strength of peatlands or erroneously indicate that a peatland is a net atmospheric C sink, when, it may actually be a net source.

Climate change and peatland carbon cycling

Peatlands have traditionally been viewed as a net sink for atmospheric CO_2 throughout the millennium. However, it is uncertain whether peatlands can continue to absorb and sequester atmospheric CO_2 under changing climatic conditions. The balance between CO_2 uptake and release can be so close that a small change in water table, temperature, timing of spring thaw, senescence, or early winter snowfall could increase short-term decomposition over plant production (Bubier et al. 2003b, Le Dizes et al. 2003).

The dominant model for terrestrial ecosystem response to climate change is that increased soil temperature will lead to more rapid organic matter decomposition and subsequent soil C loss (Cao and Woodward 1998). However, the actual response of soils depends on many factors in addition to temperature-mediated C loss, in particular plant communities that provide C to the soils (Bubier et al. 2003a). Carbon dynamics in boreal peatlands are intimately linked to nutrient cycling and this may be important to boreal peatland responses to future climate change (Jonasson et al. 1999, Hobbie et al. 2002, Robinson 2002, Schmidt et al. 2002, Weintraub and Schimel 2003). Yet, it is uncertain

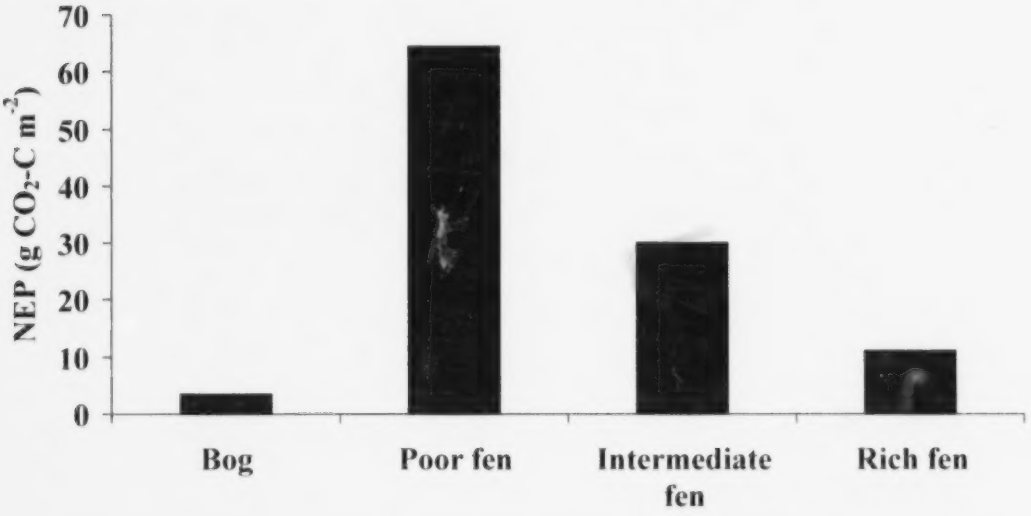

Figure 15. Net ecosystem productivity for different peatland types at Churchill, Manitoba (from Bubier et al. 1999).

whether organic matter decomposition and nutrient mineralization changes will lead to positive or negative climate change-induced feedback (Bridgham et al. 1995, 1999). For example, temperature-induced increased organic matter decomposition, resulting in high CO_2 and CH_4 output from peatlands may lead to a positive feedback of increased temperature. In contrast, increased nutrient mineralization resulting from rapid decomposition may stimulate NPP and ecosystem C gain, potentially off-setting or exceeding C losses through decomposition (Hobbie et al. 2002, Laiho et al. 2003). Thus, long-term C responses to climate change are not known.

The potential impacts of climate change on peatland C dynamics will likely be indirect through effects on vegetation community structure (Weltzin et al. 2000, 2003), NPP (Camill 1999, Laiho and Laine 1997, Laiho et al. 2003), and hydrology (Clair et al. 1998, Odland 2002). Changes in dominant plant species may change production and decomposition rates, and consequently C and nutrient cycling (Scheffer et al. 2001, Hobbie et al. 2002, Laiho et al. 2003). Some predictions indicate that deciduous species will increase and evergreen plant forms will decrease in response to climate change (Kittel et al. 2000). However, evidence for boreal and subarctic peatlands indicates that evergreen shrubs are more resilient to drought than sedges, which may lead to greater proportions of evergreen growth forms due to climate change-induced water table lowering (Camill 1999, 2000, Camill and Clark 2000, Weltzin et al. 2000, 2003, Camill et al. 2001). This can decrease organic matter quality and its decomposition over the long-term (Couteaux et al. 1995, Hoorens et al. 2002).

The importance of the link between plant phenological stage and climatic conditions on C sink/source strength has become apparent. During dry years, net CO_2 release to the atmosphere increases, especially for fens because melting of snowpacks stimulate respiration at a time when vascular plant photosynthesis has not yet started to offset CO_2 losses (Joiner et al. 1999, Lafleur et al. 2003). Climatic conditions during spring can continue to affect NEE in the fall. There can be a reduction in gross ecosystem productivity (GEP) and relatively quick transitions to plant dormancy, resulting in a net release of CO_2 in the fall during years with dry spring conditions (Griffis et al. 2000a). In years when net CO_2 release increases during the spring and fall, annual C sink/source relationships depend on the photosynthetic activities of peatland vegetation during the summer months.

If warmer and drier conditions prevail, peatlands may more frequently function as net annual CO_2 sources in the short-term (Alm et al. 1999b, Griffis et al. 2000a). If the summer is warmer, but wetter than normal, peatlands may more frequently function as C sinks because of lower soil respiration and potential

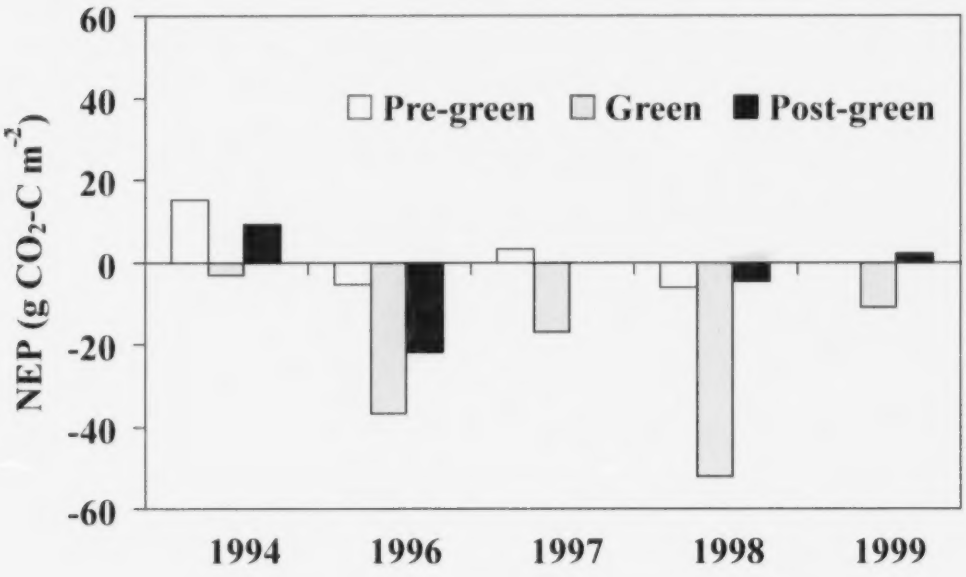

Figure 16. Mean landscape-level net ecosystem productivity by phenology for a fen located near Churchill, Manitoba (adapted from Griffis et al. 2000b).

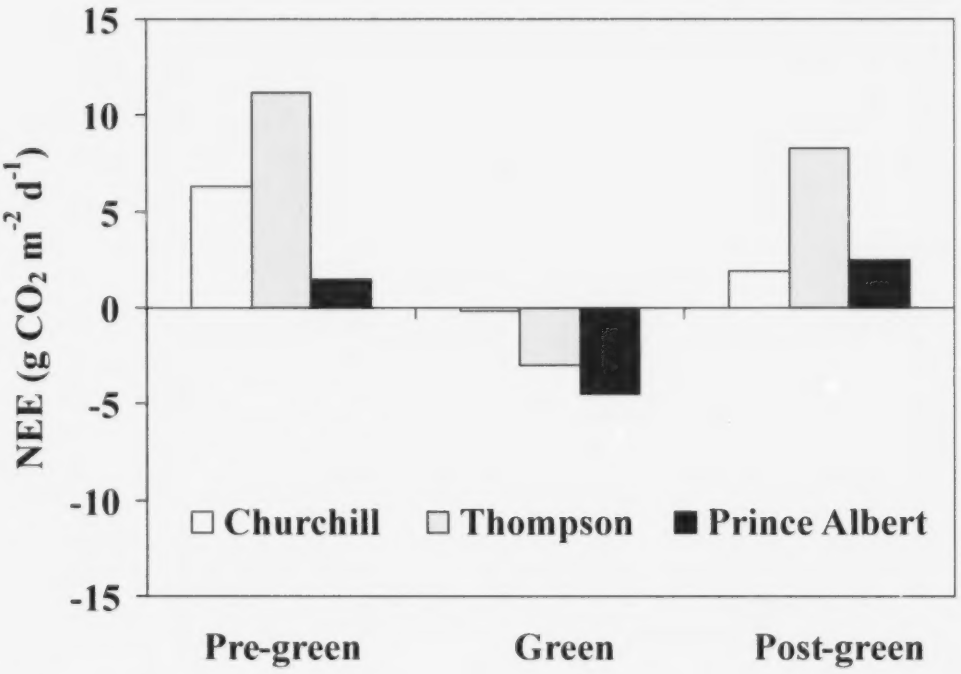

Figure 17. Net ecosystem productivity during 1994 at Churchill, Manitoba, Thompson, Manitoba, and Prince Albert, Saskatchewan fen sites (adapted from Schreader et al. 1998).

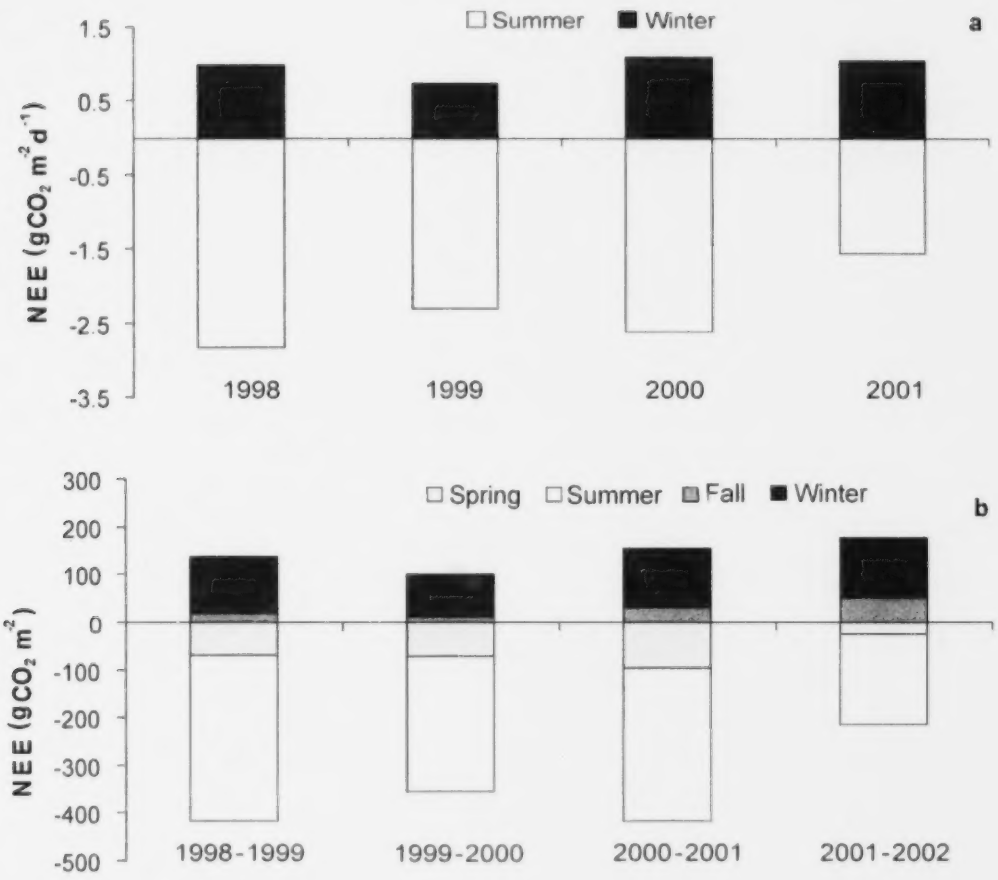

***Figure 18.** Summary of net ecosystem exchange (NEE) of carbon dioxide at Mer Bleue bog near Ottawa, Ontario; (a) Mean daily NEE fluxes in summer (June to September) and winter (December to March), (b) Seasonal NEE (adapted from Lafleur et al. 2003).*

increases in plant photosynthesis. In contrast, cooler and wetter conditions will inhibit both soil respiration and photosynthesis because of limited photosynthetically active radiation (PAR) and the peatland would become a net C source (Schreader et al. 1998). Therefore, the sink/source pattern will depend on the relative reductions in photosynthesis compared to increases in respiration. It is highly uncertain, however, how long-term peatland NEE will be affected by climate change because of multiple interacting factors (e.g., temperature, precipitation, peat and litter quality, winter snowmelt) (Moore et al. 1998, Lafleur et al. 2003). Experimentation and long-term monitoring need to be expanded to provide data that will help to refine models of climate change effects on terrestrial C sink/source relationships and sequestration.

Carbon that is transported from oxic to anoxic zones in bogs as DOC is often recalcitrant because of rather complete degradation of easily decomposable organic matter components (i.e., polysaccharides) by microorganisms in the oxic layer (Johnson and Damman 1993; Aerts et al. 1999, 2001; Scheffer and Aerts 2000). Therefore, even if changes in climate result in a lowering of the water table, and/or increased temperature of peat within the previously anoxic zones, that peat would be relatively resistant to further microbial degradation. Coupling this to the potential changes in vegetation communities to more shrubs and trees (which would produce litter of lower quality than graminoids) (Williams et al. 1998, Yavitt et al. 2000), there could be a long-term decrease in organic matter decomposition in peatlands as a result of climate change, even if temperatures increased. Should this occur, an increase in peatland C sequestration rates may occur in the long-term

Figure 19. Percentage of area occurring as peatlands and total peatland area for northeastern and northwestern Ontario (adapted from Kettles and Tarnocai (1999).

(Hobbie et al. 2002). This is an area that requires more research before appropriate predictions of peatland C responses to climate change can be developed.

Although conflicting data have been reported for C sink/source functions in northern peatlands, it is generally acknowledged that northern peatlands are sensitive to changes in climate (both temperature and precipitation). Kettles and Tarnocai (1999) determined climate change sensitivity ratings for peatlands in Canada. The sensitivity ratings for Ontario are shown in Figure 19. Peatlands occurring in the Mid and Low Boreal zone show a low to moderate sensitivity to climate change, while at higher latitudes (High Boreal and Low Subarctic zones), peatland sensitivity to climate change increases to severe or extremely severe (Kettles and Tarnocai 1999). The High Boreal and Low Subarctic regions contain most of the fen peatlands in Ontario (Tarnocai et al. 2000, 2002) and it is fens that are highly sensitive to climatic change (Kuder and Kruge 2001, Weltzin et al. 2003). Therefore, the impacts of climate change may be more regionally significant in terms of peatland functions and structure in the Hudson Bay Lowlands region of Ontario than elsewhere in the province. The Hudson Bay Lowlands are the second largest contiguous peatland in the Northern Hemisphere (Gorham 1991).

Understanding how potential shifts in vegetation affect C production and emission rates is also important to identifying how potential climate warming might alter C cycling in Ontario's peatlands. For example, if climate change invokes shifts in peatland communities, particularly in the Hudson Bay Lowlands where most fens are concentrated, would there be a relatively rapid shift from fens to bogs, and a further decrease in organic matter quality? How would these systems respond in terms of C cycling? Would organic matter decomposition be inhibited (with a resulting decrease in CH_4 production) in the catotelm because of more complete organic matter decomposition in the thicker acrotelm and subsequent transport of recalcitrant C to the catotelm? Should this occur, how would C stores in Ontario's peatlands be affected? All of these questions remain to be answered to increase our understanding of C cycling in peatlands.

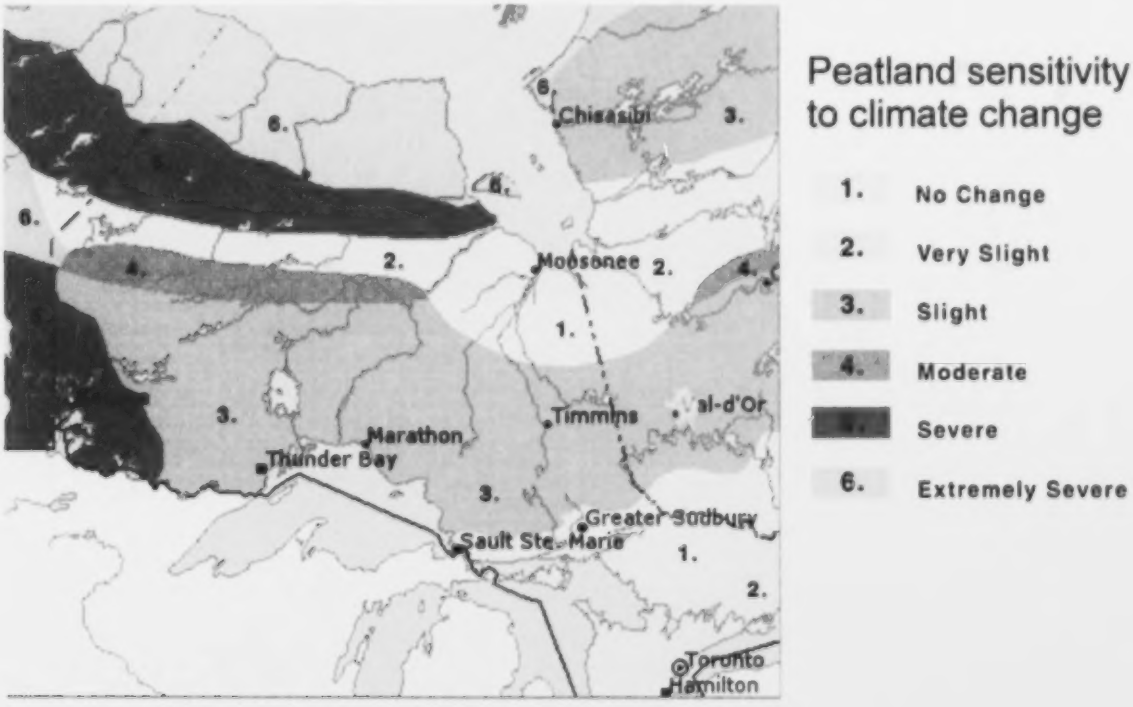

Figure 19. Percentage of area occurring as peatlands and total peatland area for northeastern and northwestern Ontario (adapted from Kettles and Tarnocai (1999).

Scaling Peatland Carbon

Approaches to scaling

Scaling difficulties

Scaling site-level measurements to regional and global levels is one of the most difficult parts of constructing global and regional inventories for predicting peatland C cycling responses to anthropogenic disturbances and their interactions, both positive and negative (Bouwman et al. 1999). Relevant spatial scales may vary from micrometers for microbial processes to global for atmospheric processes (Schimel and Panikov 1999, Middleburg et al. 1999, van Bodegom et al. 2002, Bowling et al. 2003a, Kettunen 2003, Le Dizes et al. 2003). Most scaling research has focused on trace gas (CO_2 and CH_4) fluxes, with much of the work devoted to CH_4 (Potter et al. 1996; Schimel and Panikov 1999; Walter and Heimann 2000; Potter et al. 2001; Walter et al. 2001a,b; van Bodegom et al. 2002).

Effective scaling of CO_2 NEE or CH_4 emissions to regional and global levels requires understanding spatial and temporal variability in factors driving C cycling. Most research has focused on PAR, precipitation, soil moisture, water table depth, air and soil temperature, peat and litter quality, and vegetative community structure and NPP in various combinations to describe C biogeochemical cycles (Bubier et al. 1993, 1997, 2003a,b; Bubier 1995; Hobbie et al. 2000; Walter and Heimann 2000; Frolking et al. 2001, 2002; Potter et al. 2001; Walter et al. 2001a,b; Moore et al. 2002; Saleska et al. 2002; Gould et al. 2003; Le Dizes et al. 2003). Once the influencing factors are identified, understanding the mechanisms regulating spatial and temporal patterns of C cycling processes needs to be described using models (Bouwman et al. 1999). However, it is not clear which variables are most suited for scaling. For example, water table depth is frequently identified as an important variable in scaling CH_4 fluxes (Bubier et al. 1993; Potter et al. 1996, 2001; Walter et al. 2001a,b), but in a synthesis of a 12-year study conducted in the tundra region in Greenland, Scandinavia, Iceland, and Siberia, Christensen et al. (2003) reported that mean seasonal soil temperature was a strong predictor of CH_4 flux, explaining up to 84% of the variance. Temperature combined with organic matter quality (measured as organic acid concentration, particularly acetate), explained nearly 100% of the variance in CH_4 emissions. In this study, differences in water table depth did not show any consistent predictive power of large-scale variations in CH_4 emissions. Recent global wetland CH_4 process-based models indicate the importance of understanding effects of organic matter quality and its incorporation to refine models predicting CH_4 emissions (Potter et al. 2001; Walter et al. 2001a,b). Also, because many scaling studies use process-based or semi-empirical models, a balance between pertinent forcing variables and computing resources is necessary.

Another complication in scaling C fluxes to broader scales is that different methodologies are used to collect flux data (e.g., chamber vs. flux tower vs. aircraft) and scale it up (i.e., emission factor, modelling). These differences pose major challenges in reconciling the role of peatlands in regional and global C balances (Bonan 1995). Field and laboratory studies of trace gas fluxes provide extremely variable results and are sensitive to environmental and vegetative conditions (Aurela et al. 2002, Lafleur et al. 2003, Nykanen et al. 2003). Small changes in environmental conditions can cause non-linear changes in flux rates (Middleburg et al. 1999). For example, CH_4 fluxes at a scale of < 1 m^2 may change dramatically when soil moisture levels cross thresholds, resulting in nonlinear transitions between methanogenesis and methanotrophy as the dominant process in CH_4 cycling (Schimel and Panikov 1999). These nonlinear processes and resulting fluxes make it difficult to scale trace gases (Poicher et al. 1998, Derwent et al. 1999, Middleburg et al. 1999).

Many researchers have concluded that predicting trace gas fluxes is nearly impossible at small scales because it would require detailed information on soil properties, soil microclimate, and microbial population dynamics at all locations for which predictions are made (Bouwman et al. 1999). In contrast, some analyses indicate that patterns of trace gas fluxes at broader levels, especially when aggregated to weekly or longer intervals may be more predictable than small-scale approaches (Derwent et al. 1999). This is because integrated fluxes at some scales may be a function of substrate availability and "average" biophysical (e.g., leaf area index (LAI), stomatal conductance, albedo, sensible and latent heat) conditions (Bonan 1995, Bouwman et al. 1999). Thus, deriving flux estimates for processes occurring at scales smaller than needed to answer questions should not be a focal point because of ineffective allocation of limited resources and potential imbalances in detail and scale among different model components (Middleburg et al. 1999).

Scaling methods

Peatland C scaling research has focused on 3 spatial scales: landscape, regional, and global. The latter 2 scales advocate including peatlands in land surface schemes (LSS) or land surface models (LSM) that can be coupled to GCMs (Letts et al. 2000; Frolking et al. 2002; Bowling et al. 2003a,b). Landscape scaling of peatland C dynamics has been conducted using (1) fine-scale to meso-scale topographic relationships within a landscape with CH_4 or CO_2 collected with flux chambers and scaled using aerial coverage (i.e., emission factor approach) of the various topographic components (Waddington and Roulet 1996, Kettunen 2003), (2) landscape-scale micrometeorology with CO_2 measured using flux towers (Vourlitis and Oechel 1997, Griffis et al. 2000a, Friborg et al. 2003), and (3) vegetative community structure with CH_4 and CO_2 measured with flux chambers and scaled using the emission factor approach (Bubier et al. 1993, Bubier 1995, Reeburgh et al. 1998).

Regional and global scaling of peatland C dynamics may involve using remote sensing (aircraft- and satellite-based sensors), vegetative cover types, environmental data (e.g., water table depth, peat temperature) and the coupling of various models (Stow et al. 1998, Loiselle et al. 2001, Chen et al. 2002, Prasard et al. 2002, Thomas et al. 2002, Boelman et al. 2003, Gould et al. 2003, Schmidt and Skidmore 2003, Takeuchi et al. 2003, Wagner et al. 2003). Bouwman et al. (1999) recommended that where possible, flux models be used to replace traditional emission factor approaches. Process-based or semi-empirical models are preferred over empirical models for LSS applications (to produce spatial and temporal distributions).

Global Circulation Models are providing a more thorough understanding of spatial and temporal variation of processes occurring at sub-grid (e.g., <1 km^2) scales; the understanding of those processes are being linked to LSS and subsequently used to advance GCMs (Polcher et al. 1998, Delage et al. 1999, Bartlett et al. 2002, Bowling et al. 2003a, Nijssen et al. 2003). Peatland C dynamics should be scaled with the overall goal of incorporating the scaling method into LSS, which can be coupled to GCMs (i.e., Letts et al. 2000, Frolking et al. 2002). This implies that peatlands need to be evaluated in relation to other cover types within a landscape or region. This is critical because although the peatlands within a landscape may act as a net sink of atmospheric C, the dynamics of other landforms and vegetation cover types within the landscape may cause the area to be an overall net source of atmospheric C, or the reverse may be true.

There are 2 basic approaches for scaling biogeochemical fluxes: bottom-up and top-down (Bouwman et al. 1999, Derwent 1999). The approaches are represented schematically in Figure 20. Bottom-up approaches are calculated from smaller to larger scales and involve extending calculations from easily measured and reasonably well understood units to more encompassing processes. Various challenges are associated with bottom-up scaling, including how best to aggregate spatial and temporal variation of fluxes, which data to use, and how to translate mechanisms and processes between different scales (Derwent et al. 1999, van Bodegom et al. 2002). Top-down scaling involves using measurements made at broad scales, setting boundary conditions for specific problems, and then testing general relationships for specific cases (Potter et al. 1996, Fung et al. 1997, Cao et al. 1998, Joos et al. 2001, McGuire et al. 2001, Gosh and Brand 2003, Scholze et al. 2003). Examples of observations at a higher level of scale that are used to constrain flux estimates include atmospheric concentration and mixing ratios of stable isotopes (Fung et al. 1997, Trumbore 1999). Top-down scaling can be very useful for testing hypotheses and identifying missing information (Bowman et al. 1999).

Bottom-up scaling is the more common approach and methods used to scale information include aggregation, generalization, stratification, and modelling (Bouwman et al. 1999). Aggregation involves collecting and linking information into an aggregate unit. Aggregated results can be presented as the mean or median value coupled with statistical information, such as standard deviation. Generalization involves describing a group using properties of a sub-unit that is considered to be representative based on expert knowledge. This method is used when observational or statistical data on individual members of a group are scarce. Stratification subdivides an aggregate into components, for example into functional units with similar properties and environmental and management conditions that regulate biogeochemical fluxes (Seitzinger et al. 1999). Modelling breaks down a system into its main components and describes the behaviour of the system through their interaction. Stratified sampling is the most commonly used method and is often combined with remote sensing and/or process- or semi-empirical models.

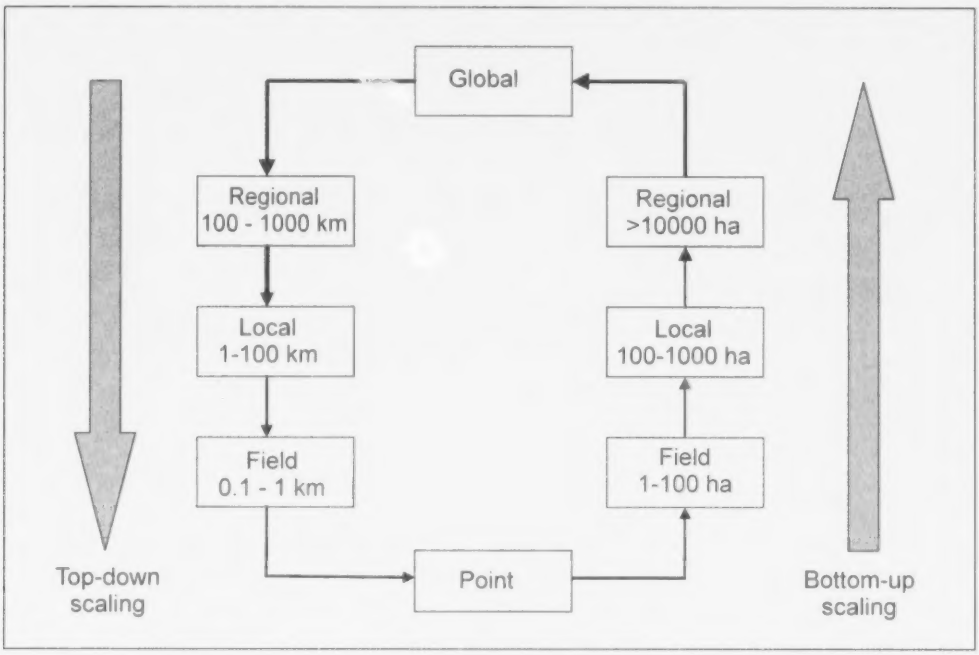

Figure 20. *Diagram showing the top-down scaling approach with its hierarchy of models (inverse models) and the bottom-up approach with the various forward (direct) models (adapted from Derwent et al. 1999).*

Carbon scaling research at both regional and global levels is beginning to emphasize the use of functional types (i.e., groups of C-cycle controlling variables). Functional relationships (between controlling variables and C fluxes) are defined, then combined with spatial information on the distribution of controlling variables across temporal and spatial scales of interest (IGBP 1996, Estes and Loveland 1999, Seitzinger et al. 1999) (Figure 21). Use of functional types differs from the more conventional approach that identifies regions based on vegetation composition (Seitzinger et al. 1999). An advantage of the functional type approach is that C fluxes are not related specifically to vegetative cover types. Thus, functional relationships are better suited for larger-scale modelling of C fluxes than vegetation community composition alone (IGBP 1996, Estes and Loveland 1999, Seitzinger et al. 1999).

The remainder of this section will discuss (1) the emission factor approach and (2) modelling to scale fluxes to regional and global levels, because these are the most common scaling approaches (Bouwman et al. 1999). Knowledge gaps are identified and recommendations are made about environmental and/or ecosystem community data needed to improve understanding of up-scaling data. The discussion on modelling fluxes does not focus on the development of algorithms (references are provided for those interested in pursing that topic), but presents a conceptual basis for including specific driving variables.

Emission factor approach

In emission factor approaches, emission estimates are derived by combining measurement data with geographical and statistical information of ecosystem processes:

$$E = A_x E_f \qquad \textit{Eq. 8}$$

where E is the emission, A_x is the area of functional units (e.g., land cover, topographic position, management unit) and E_f is the emission factor (e.g., g CO_2-C m^{-2} yr^{-1}). When using the emission factor approach, both the stratification scheme for delineating functional types and the reliability of the emission factor determines the accuracy of the flux estimate (Bouwman et al. 1999).

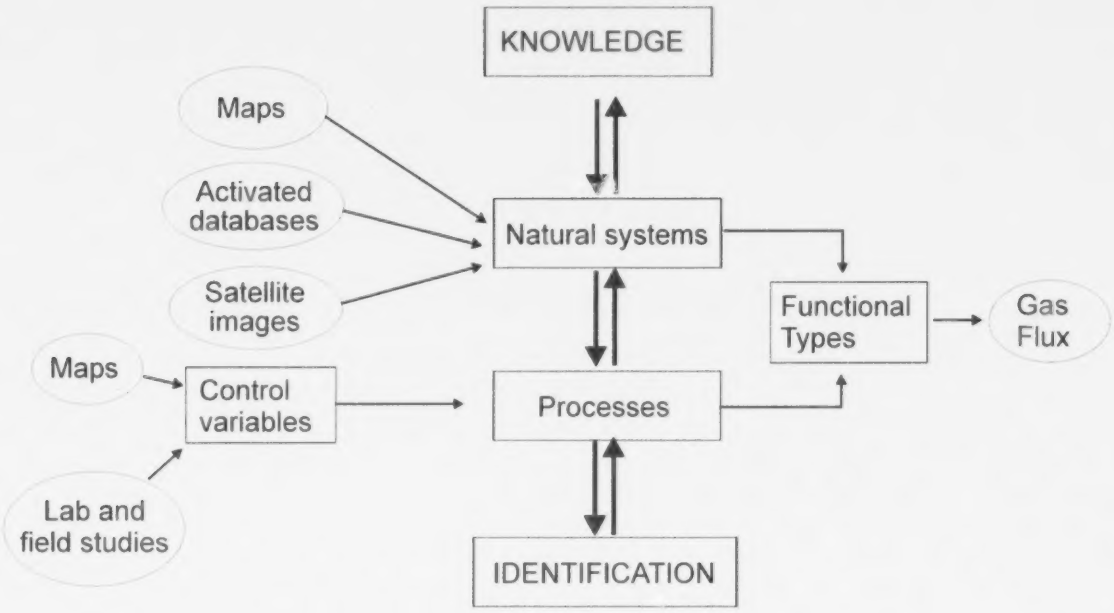

Figure 21. Relationships between key parameters and functional types for assessing trace gas fluxes (adapted from Seitzinger et al. 1999).

Several studies have used the emission factor approach to extrapolate CO_2 NEE and CH_4 emissions from the site-level to the landscape or regional scale (Bubier et al. 1993, Roulet et al. 1994, Waddington and Roulet 1996, Reeburgh et al. 1998, Prasard et al. 2002, Takeuchi et al. 2003). Reeburgh et al. (1998) developed a CH_4 emission estimate for the Kuparuk River Basin in Alaska. They used static chambers to measure CH_4 fluxes from sites representing different vegetation types. Regional CH_4 flux was calculated from a hierarchical geographic information system (HGIS). The Kuparuk River Basin land cover map (extracted from an existing mosaic of Landsat multispectral scanner (MSS) frames) was used to display the distribution of CH_4 flux based on measurements from the vegetation types. The CH_4 emission from each land cover category was summed to obtain an emission estimate for the total area. The results were used to project the CH_4 emission contributions of the Arctic region.

Using aerial coverage, Reeburgh et al. (1998) found that peatland area was underestimated by 30% in land classifications developed using Landsat MSS. Because many peatlands are typically small, estimations of peatland areas decreased with the larger pixel sizes available from satellite sensors. Furthermore, many peatland areas border streams with dimensions that are smaller than pixel sizes, so these could also be misclassified or missed. They concluded that uncertainties in regional estimates were linked to peatland and open water emissions and that, because of potential misclassification of high-emission categories, CH_4 emission predictions are no better than $\pm$50 to 75%.

Reeburgh et al's. (1998) results were comparable to an independent estimate of CH_4 emissions from the Toolik Lake area of Alaska conducted by Shippert (1997). Shippert's (1997) study focused on 3 images of the Toolik Lake area, derived from a SPOT MSS image, European Remote Sensing Satellite (ERS-1), and synthetic aperture radar (SAR), plus a digital elevation model (DEM) based on aerial photographs. Shippert (1997) linked CH_4 emissions to environmental conditions using the functional type approach rather than vegetation types. Shippert (1997) estimated 750 mg CH_4 m^{-2} yr^{-1} emission compared to the 645 mg CH_4 m^{-2} yr^{-1} calculated by Reeburgh et al. (1998).

Waddington and Roulet (1996) measured CH_4 and NEE measurements at 3 spatial scales along transects in Sweden. They examined C exchange over spatial

scales from tens of centimetres (microtopography; hummocks and hollows) to tens of metres (mesotopography; lawns and ridges) to hundreds of metres (macrotopography; floating mat, hinge, plateau, margin). The general trend was that topographically lower and wetter areas, such as hollows, pools, or peatland margins, emitted more CH_4 and absorbed less CO_2 than the adjacent higher and drier areas, such as hummocks, ridges, and plateaus. These trends indicate opposite patterns for CO_2 uptake and CH_4 emission in relation to peatland hydrology and that the pattern was similar for all 3 hydrological scales.

They reported that a combined mesoscale topographic model (MMF) best estimated total peatland CH_4 emission and CO_2 exchange. The MMF produced similar estimates for peatland ecosystem-level exchange of CH_4 (5.2 and 5.5 g CH_4 m^{-2}) relative to the MEF (microtopographic model) and MAF (mesotopographic model) estimates during 2 years. Estimates of ecosystem NEE, however, differed greatly among models. The MMF provided estimates of -35. 5 and -4.2 g CO_2 m^{-2}, while the MEF estimates were -17.3 and 38.8 g CO_2 m^{-2}, and MAF estimates were 33.8 and 171.1 g CO_2 m^{-2}. Therefore, for NEE, the method used to extrapolate site-specific fluxes can provide very different results. Waddington and Roulet (1996) also reported that the model indicates that failing to measure the exchange of C from peatland pools can result in overestimating total peatland NEE of CO_2 and therefore also overestimating C accumulation rates.

Bubier et al. (1993) calculated regional CH_4 flux from the Clay Belt area of northeastern Ontario. They used annual mean CH_4 flux from different peatland types and subformations within a peatland type. Regional CH_4 emission rates were estimated using mean CH_4 flux determined from static chambers and applying a season length of 150 days (mid-May to mid-October) to approximate annual CH_4 emissions. Annual fluxes for each peatland subformation (e.g., open bog, treed fen) were then weighted based on average proportion of each peatland type reported in the Ontario Peatland Inventory (Riley 1994). They estimated that habitat-weighted CH_4 flux from Clay Belt peatlands was 3.4 g m^{-2} yr^{-1}. The flux for the entire Clay Belt region was estimated at 0.7 g m^{-2} yr^{-1} assuming 21% peatland coverage (Riley 1994). About one-half of the emissions were estimated to be from conifer swamps, which cover 58% of the peatland area. However, because of large differences in ecological type within the conifer swamp class (Jeglum 1991), the aerial estimate of wet versus dry swamps may be skewed by 50% or more.

Bubier et al. (1993) reported 3 probable sources of error in their study: sampling error, over- or underestimation of peatland area, and classification error. They reported a combined error estimate of 56% for the annual CH_4 flux from the Clay Belt peatlands, indicating habitat-weighted annual CH_4 flux emissions could range from 1.47 to 5.28 g m^{-2} yr^{-1}. The most serious source of error was the difficulty of estimating CH_4 flux using the broad-scale classification of the Ontario Peatland Inventory (Riley 1994). This type of classification is well suited for large-scale estimates of peatland type by vegetation and trophic status (Zoltai et al. 1988) across wide geographic areas. However, the classification is not detailed enough for estimating CH_4 flux (Bubier et al. 1993). In the Clay Belt, conifer swamps are the dominant peatland type, and have the widest range in ecological attributes and seasonal CH_4 flux. Bubier et al. (1993) estimated that the error associated with diversity of conifer swamps alone was responsible for 43% of the total error in annual flux estimates for the Clay Belt. They suggested that for classifications to be useful for CH_4 predictions, they must incorporate hydrology and microtopography. This is a particular problem for forested peatlands where understory vegetation, which is a better indicator of water table position than tree cover, is difficult to detect using remote sensing (Jeglum 1991). However, recent advances in remote sensing technologies, such as SAR, may help (Pope et al. 1997, Saatchi and Rignot 1997, Townsend and Walsh 2001, Toyra et al. 2001, Townsend 2002).

Takeuchi et al. (2003) used remote sensing techniques to scale regional peatland CH_4 concentrations in Siberia. They used a SPOT high resolution visible (HRV) image supplemented by field observation to map 4 ecosystems (birch forest, conifer forest, forested bog, and open bog). Field observations were then scaled up using 3 spatial resolutions of satellite data. Each of the peatland ecosystem coverage fractions at the sub-pixel level was provided by spectral mixture analysis between NOAA advanced very high resolution radiometer (AVHRR) and SPOT HRV images acquired on the same day. A mean rate of CH_4 emission of 21.1 mg CH_4 m^{-2} d^{-1} from forested bog and 233.1 mg CH_4 m^{-2} d^{-1} from the open bog were calculated from field observations. The CH_4 emission from the area was estimated by multiplying these average emission rates and the fractional coverage in each AVHRR pixel. Using this

emission factor approach, total CH_4 emission over AVHRR coverage was estimated to be 9.46×10^{9} g CH_4 m^{-2} d^{-1} and the mean emission over AVHRR coverage was calculated as 59.3 mg CH_4 m^{-2} d^{-1}, which is within the range of probabilistic variability computed using airborne measurements.

Although scaling based on the emission factor approach has been successful in some regions, it may be inadequate in others because gradients in plant communities within ecosystems or microtopographic differences in hydrology (which are important for explaining spatial variability in CO_2 and CH_4 flux) are not adequately incorporated (Bubier et al. 1993, Kettunen 2003). Dominant biogeochemical processes that control CO_2 NEE or CH_4 flux in peatland classification systems have also not been adequately integrated. For example, in the boreal region, forested peatlands have wide ranges in CH_4 emission because of varying moisture and temperature conditions within the overall category of forested peatlands (Bubier et al. 1993), which are the dominant peatland type in Ontario (Riley and Michaud 1987, Zoltai et al. 1988, Bubier et al. 1993, Riley 1994, Bubier 1995). Because of the range of ecological conditions in forested peatlands, these systems may be better suited for scaling using process-based models that account for water table depth, organic matter quality, peat temperature and moisture, and meteorological variables.

Modelling

A number of modelling approaches have been used to scale C cycling to landscape, regional, and global levels (Potter et al. 1996, 2001; Potter 1997; Schimel and Panikov 1999; Walter and Heimann 2000; Grandberg et al 2001; Walter et al. 2001a,b; Grant and Roulet 2002; Frolking et al. 2002; van Bodegom et al. 2002). Although a high degree of international interest exists in incorporating wetland models into GCMs (IPCC 2001), this subsection discusses only the approach being developed in Canada. This approach is coupling process- and semi-empirical-based models of peatland C cycling to the Canadian Land Surface Scheme (CLASS), and subsequently to the Canadian Coupled Climate Model (C^3M). First, LSSs will be discussed in general to highlight their capability and current weaknesses in simulating various landscape functions. Then, the methodology being used in Canada to couple peatland C models to CLASS and C^3M is highlighted.

Land surface schemes: general description: Current atmosphere models are solved spatially on a 3-dimensional grid of points on the globe with a horizontal resolution of 250 km and some 10 to 30 vertical levels (IPCC 2001). Processes occurring at spatial and temporal scales smaller than the climate model's resolution are coupled to the climate model. A realistic representation of coupling between models is critical to adequately project climate change and potential interactions. Land surface schemes are one of the approaches used to couple smaller scale spatial and temporal processes to the more complex climate models (IPCC 2001). Land Surface Schemes include parameters such as soil, topography, vegetation, snow, permafrost, and land ice (Polcher et al. 1998).

The effects of small-scale heterogeneity in land surface characteristics (e.g., soils, snow, vegetation, topography) on large-scale fluxes of water and energy have been a focal point of biogeochemical scaling over the past decade (Delage et al.1999; Bowling et al. 2003a). One problem is that climate models use large grid cells with high heterogeneity, and have difficulties in averaging various components of a grid cell without bias. Surface parameters are commonly aggregated to generate effective values representative of the entire grid cell of an area (Derwent et al. 1999). At times, however, parameter aggregation is not possible and surface fluxes must be calculated separately for a number of sub-areas inside a grid cell (the mosaic approach). To reduce computational cost, it is important to determine the degree of complexity required to provide acceptable estimates of aerial coverages. This can lead to difficulties in coupling multiple LSSs into climate models.

A vast array of LSSs are used worldwide (e.g., Bowling et al. 2003a,b; Nijssen et al. 2003) and many international comparisons of LSSs have been conducted [i.e., the Project for the Intercomparison of Land Surface Parameterization Schemes (PILPS), the Global Soil Wetness Project (GSWP), the International Satellite Land Surface Climatology Project (ISLSCP), and the Biological Aspects of the Hydrological Cycle (BAHC) (e.g., Henderson-Sellers et al. 1996, Polcher et al. 1998, Bowling et al. 2003a, Nijssen et al. 2003). Significant progress has been made in incorporating physical processes into LSSs (IPCC 2001). However, there are difficulties in the ability of LSSs to partition available energy between sensible and latent heat and partition available water between evaporation and

runoff (Bowling et al. 2003a,b; Nijssen et al. 2003). In addition, LSSs have limited capability to simulate incoming solar radiation, soil moisture, and hydrology (IPCC 2001).

Snow, and the snow albedo feedback, are important components of the land surface. Current climate models incorporate snow in varying degrees of sophistication and there are currently major uncertainties in the ability of LSSs to simulate snow mass or snow cover (IPCC 2001). Frei and Robinson (1999) evaluated the simulation of monthly snow extent from 27 Atmospheric General Circulation Models (AGCMs) and found weaknesses in the simulation of the seasonal cycle of snow extent and a general underestimation in interannual variability. These weaknesses limit confidence in the simulation of high latitude changes predicted by current climate models because the failure to accurately simulate snow affects on albedo, surface roughness length, and soil moisture (Bowling et al. 2003a, Nijssen et al. 2003). Other components of the land surface that are potentially important to climate change but have not easily been simulated accurately include lateral water flows, water storage, permafrost, and land-ice (IPCC 2001). Tremendous effort is going into refining modelling capabilities in those areas.

Canadian Land Surface Scheme: In Canada, the LSS currently being used is CLASS. It is a 4-patch mosaic, biophysical LSS, developed at the Meteorological Service of Canada, for use in the C^3M (Verseghy 1991). CLASS provides a 1-dimensional parameterization of land surface processes, incorporating a simple treatment of sub-grid-scale heterogeneity. Each cell is represented by 1 to 4 subareas, representing bare soil and vegetated areas, with and without snow cover, which are all treated separately. Four vegetation categories are recognized within the vegetation subarea: needleleaf trees, broadleaf trees, crops, and grass. Further details of the vegetation categories of CLASS can be found in Verseghy (1991) and Wang et al. (2002). The remainder of this discussion will focus on the soil and hydrological aspects of CLASS.

The soil parameter in CLASS is divided into 3 layers of 0.10, 0.25, and 3.75 metre thickness; heat flow between layers is modelled using thermal diffusion theory, water transfer between layers is based on infiltration, with the Darcy theory used for drainage (Bartlett et al. 2002). CLASS's initial soil parameterization was for mineral soil; however Letts et al. (2000) added an organic soil parameterization, defining the hydraulic properties of fibric, hemic, and sapric peat. Bartlett et al. (2002) investigated the effects of soil heterogeneity on CLASS. They reported that a 2-patch mosaic, consisting of 1 patch of sandy soil and 1 with 2 peat layers over clay, essentially duplicated the results of the 4-patch mosaic run using data from the BOREAS northern study site. They also indicated that a detailed analysis of surface feedbacks is required when modelling the effects of changes in soil temperature and moisture on the C balance. Longer-term studies are required to more fully evaluate the ability of the 2 methods to represent the water balance on an annual basis, and/or the effects of errors in the long-term water balance of the turbulent fluxes (Bartlett et al. 2002).

CLASS also has a hydrologic component. Soulis et al. (2000) used CLASS to simulate hydrology at the watershed scale. The simulations linked CLASS to vertical hydrology with the Waterloo Flood Forecasting Hydrological (WATEFLOOD) model (Kouwen 1988). The linked model, WETCLASS, has been used to simulate conditions for snowmelt runoff (Fassnacht et al. 1999). Fassnacht and Soulis (2002) attempted to improve hydrological process representation within CLASS. Although, they reported changes in the simulation of a number of hydrologic and climate variables were small and did not improve simulated streamflow, they may be important during transitional periods such as initial accumulation and depletion of snow-covered areas during snowmelt. The hydrological parameterization for peatlands conducted by Letts et al. (2000) was validated for water table depth and peat temperature at a fen in northern Quebec and a bog in northcentral Minnesota.

The CLASS model was part of the PILPS-Phase (2e) experiment (Bowling et al. 2003a,b). This study was conducted on high-latitude hydrological process simulations using prescribed atmospheric conditions to drive the LSSs. In addition, there were no mechanisms to represent interactions between land surface and the atmosphere (Bowling et al. 2003a). The objective of PILPS-Phase (2e) experiment was to "evaluate" the performance of uncoupled LSSs in high latitudes to assess their ability to capture key processes spatially. The Torne and Kalix River basins in Scandinavia were used for PILPS-Phase 2(e) testing (Bowling et al. 2003a,b). The results indicated highly variable simulations of small high-latitude catchments dominated by peatlands performed by 21 LSSs (including CLASS) (Bowling et al. 2003a, Nijssen et al. 2003), which may have limitations for hydrological simulations within Ontario. CLASS overestimated mean monthly discharge when compared to observed values for the Torne and Kalix Rivers. In

addition, CLASS overestimated peak streamflow early in snowmelt, underestimated discharge duration during snowmelt, and simulated results varied from observed flows. One of the reasons was that calibration was not transferred from sub-basins to the regional scale (Bowling et al. 2003a, Nijssen et al. 2003). CLASS was able to capture the limitations imposed on annual latent heat by the small radiation available to the high latitude Torne and Kalix River Basins (Bowling et al. 2003a).

Peatland Carbon Simulator (PCARS) and its coupling to CLASS: The brief discussion about PILPS-Phase 2(e) was relevant because there is a major effort, in addition to the peatland hydrological parameterization by Letts et al. (2000), to couple a process-based peatland C model, the Peatland Carbon Simulator (PCARS) to CLASS (Frolking et al. 2002). Peatland hydrology is a major driver of peatland C cycles and effective interfacing of both C simulations by PCARS and snowmelt by CLASS will be crucial for accurate scaling of climate change and C cycling feedbacks across Canada.

The Peatland Carbon Simulator is a process-oriented model of the contemporary C balance of northern peatlands that simulates the C balance of a peatland over seasonal to multiyear timeframes (Frolking et al. 2002). Initial parameterization of PCARS is being conducted with data from the Mer Bleue Peatland complex. PCARS has been designed to link with CLASS to examine climate-peatland feedbacks at regional scales in future analyses but coupling is not yet complete. Components of PCARS are (1) vascular and nonvascular plant photosynthesis and respiration, net above- and belowground production, and litterfall, (2) aerobic and anaerobic decomposition of peat, (3) production, oxidation, and emission of CH_4, and (4) DOC loss with drainage water (Frolking et al. 2002). PCARS includes submodels to (1) initialize the entire peat profile based on a long-term mean accumulation using the Peat Decomposition Model (PDM) (Frolking et al. 2001), (2) simulate hourly vegetation photosynthesis and respiration, (3) simulate hourly aerobic and anaerobic decomposition down the peat profile, and (4) simulate daily, seasonal, and annual vegetation phenology, C allocation, NEE, CH_4, and DOC fluxes from the peatlands and to simulate NEP (Frolking et al. 2002). PCARS has an hourly time step and requires air and soil temperatures, incoming radiation, water table depth, and horizontal drainage as drivers. Simulations predict a complete peatland C balance for one season to several years (Figure 25).

To simulate the C balance of a particular peatland, PCARS requires site-specific data in 3 categories. First, the model requires data for initializing the peat profile, which is obtained from PDM (Frolking et al. 2001). This algorithm requires values for the basal date of the peat, peat bulk density, and long-term mean vegetation NPP of each plant type. The second required data set is a site-specific description of the vegetation: maximum and minimum foliar biomass, tissue photosynthetic rate, above-/belowground biomass ratios for the vascular plants, DOC concentrations in water draining from the peatlands, and a depth range for CH_4 oxidation. The third site-specific data set required is hourly (or daily) weather data to drive the simulations: air and soil temperatures, water table depth, incoming PAR, relative humidity, and water runoff. Weather station data could be used to drive a peat soil climate model (Frolking et al. 2002). An additional set of parameters, based on values in the literature, are not site-specific, and are expected to be constant across simulations of a range of northern peatlands.

Frolking et al. (2002) suggested that the major sources of uncertainty in model parameterization are related to controls on decomposition. These include (1) the appropriate water table depth for comparison between modelled and measured values, including microtopography, (2) the impact of peat water content on decomposition, which is a function of water table depth and peat structure, (3) the initial mass loss rates for belowground tissues (fine roots), (4) the effect of long-term anoxia on suppressing decomposition in deep peat, and (5) the parameterization of an increase in recalcitrance as organic matter decomposes. This group is continuing to refine PCARS.

After further testing at other instrumented northern peatland sites in North America and Eurasia, PCARS will be extended to regional and global-scale simulations (Frolking et al. 2002). Challenges in extrapolating PCARS to larger scales are related primarily to mapping vegetation communities of northern peatlands (peatlands are not well mapped in many areas). Another challenge will be how to measure or simulate the spatio-temporal dynamics of peatland water table depth across the range of northern peatlands. Remote sensing can be used to map inundation at large scales and with high resolution (e.g., Toyra et al. 2001), but is less useful for mapping water tables below the surface.

The Ontario Ministry of Natural Resources (OMNR) should be an active partner in refining PCARS and coupling it to CLASS. The OMNR should also become more actively involved with the Experimental Lakes Area studies on peatland biogeochemistry. The Ontario Forest Research Institute (OFRI) could be the lead institute in parameterizing and validating PCARS for forested peatlands by both resurrecting the Walley Creek study site and using the White River Riparian Zone study site. Funding could be sought from the Climate Change Network, Fluxnet-Canada, or other programs to support the work. The Ontario Forest Research Institute is already directly involved with Fluxnet-Canada, where they are conducting soil C research and collaborating with universities and federal agencies across Canada. In addition, OFRI is part of a binational forested wetland research network with the US Forest Service and Michigan Technological University that could be expanded to include the University of Minnesota and University of Wisconsin in support of this initiative.

The OMNR could also be the lead agency in developing peatland ecosystem classifications for Ontario that would be conducive to regional and national scaling efforts using PCARS-CLASS-C'M coupling.

Summary and Recommendations

Summary

Locating and understanding the spatial and temporal distributions of CO_2 and CH_4 sources and sinks are necessary to predict their responses to management interventions or climate change. This important issue has key global economic and political implications. Peatlands are important to the atmospheric C balance, and research over the past 2 decades has significantly reduced uncertainties in understanding peatland C cycling. However, critical knowledge gaps regarding C sources and sinks remain to be understood before adequate predictions that relate peatland C sources and sinks to regional, national, and global C budgets are possible.

Peatland area in Ontario is about 312,780 km^2, representing 93% of the total provincial wetland area and about 30% of the provincial land base. Preliminary estimates calculated here indicate that Ontario's peatlands contain 41.7 Pg C, representing potentially up to 25% of the C stored in Canada's peatlands and about 10% of the C stored in northern peatlands worldwide. Conifer swamps are the dominant peatland type in Ontario and account for 53% of the peatland area across the province. Conifer swamps and bogs together account for greater than 80% of Ontario's peatland area. Based on these and other parameters (i.e., peat depth, decomposition class, bulk density), conifer swamps contain about 58% of the total peatland C density in, and contribute about 42% of the CH_4 flux from, Ontario's boreal peatlands. Total CH_4 flux from Ontario's peatlands, however, are one of the lowest in the Northern Hemisphere, accounting for only about 2 to 5% of the total CH_4 burden to the atmosphere from northern peatlands.

Northern peatlands are sensitive to climate change and published information indicates that some peatlands more frequently act as net sources of atmospheric C than in the past, at least in the short-term. In Ontario, peatlands occurring in the High Boreal and Low Subarctic zones appear to be very sensitive to climate change. These 2 zones contain the Hudson Bay Lowlands region, which is the second largest contiguous peatland in the Northern Hemisphere, and may undergo the highest rate of change in peatland C cycles. In addition, Ontario's boreal forest currently functions as a net source of atmospheric C because of high fire frequency in the boreal landscape of Ontario (Kling et al. 2003). Thus, peatland C sequestration may fill a critical niche that helps reduce the atmospheric C burden from the boreal forest in Ontario. Thus, understanding the role of Ontario's peatlands in the sink/source and C sequestration function of Ontario's boreal landscape is critically important.

Peatland microtopography contributes significantly to spatial and temporal variability in peatland C cycling. In the spring, snowmelt and soil thawing occur earlier on hummocks than lawns or hollows. For peatlands dominated by vascular plants, hummocks are commonly net atmospheric C sources immediately after snowmelt. However, where bryophytes are dominant, they begin to photosynthesize without delay after snowmelt and, therefore, function as a net atmospheric C sink in the spring. Timing of snowmelt and soil thaw is important to both CH_4 and CO_2 cycles, with increases in net efflux of both gases potentially occurring in late winter/early spring and late fall/early winter, timeframes during which assessments rarely occur. Shifting climatic patterns may result in photosynthetic C gains that are inadequate to offset C losses due to longer and more intense heterotrophic respiration in late winter/early spring or late fall/early winter. Thus,

peatlands may become a short-term net C source to the atmosphere. The long-term impacts of climate change, however, are not straightforward or well documented. Short- and long-term trends in peatland C dynamics should be priority research areas because many climate models predict warmer, drier summers, later winter snowfall and earlier spring snowmelt, as well as more frequent rain events during winter and more intense rain events during the summer, all of which will affect peatland C cycles.

The net C sink/source strength of peatlands will also depend on the interactions of organic matter quality with precipitation and temperature. Although an increase in the C source strength of northern peatlands in response to climate change has been proposed, and studies indicate that this may be the case in the short-term (e.g., Silvola et al. 1996, Lafleur et al. 1997, Griffis et al. 2000b), the quality of peat and fresh organic matter (e.g., root exudates, litter) can override climatic variables (e.g., Belyea 1996; Hobbie 1996; Aerts et al. 1999, 2001; Christensen et al. 2003). This is one of the main reasons for inconsistent results when environmental conditions (i.e., temperature, precipitation, depth to the water table) are related to CH_4 emission. In addition, should CO_2 become a 'luxury' compound for plants due to elevated atmospheric CO_2 concentrations relative to N, phosphorus (P), or micronutrients, an increase in polyphenol concentrations of foliage and litter is likely to occur, further reducing litter quality and organic matter decomposition rates (e.g., Cotrufo et al. 1998, Northrup et al. 1998, Hattenschwiler and Vitousek 2000). Use of C and hydrogen stable isotopes, along with ^{14}C can provide valuable insight about the type of organic matter being used by microorganisms for energy production and release of CO_2 and CH_4 due to autotrophic and/or heterotrophic respiration.

For regions of Ontario that support numerous fens, such as the Hudson Bay Lowlands, a more rapid progression in peatland succession from fens to bogs may occur due to climatic-change induced lowering of water tables. Accompanied by these successional changes in vegetation, will be changes in fresh organic matter quality and its decomposition. Vegetative shifts from sedges to shrubs and conifers may increase the polyphenol content of litter, with subsequent decreases in organic matter decomposition. This may increase the C sequestration potential of peatlands in Ontario over the long-term.

Some models predict reductions in the amount of peat due to increased decomposition. However, because organic matter in bog and conifer swamp peatlands is of relatively low quality for microbial degradation, losses of peat in those peatlands may not occur to the same extent as in fens, which generally contain higher quality surface peat. Furthermore, peat in the catotelm of bogs and conifer swamps is usually more recalcitrant because of thicker acrotelms and more complete organic matter processing by microbial communities compared to fens. Therefore, the deeper peat of fens would likely be more susceptible to C losses from climate-change induced increases in microbial peat degradation than that in bogs and conifer swamps. Rapid successional changes from open and shrub bogs to conifer swamps may also increase the C sink potential of Ontario's peatlands because of greater C storage in above- and belowground biomass in trees compared to shrubs. This is the general trend reported for drained peatlands in Finland (e.g., Laiho and Lane 1997, Minkkinen and Laine 1998, Nykanen et al. 1998, Laiho et al. 2003)

Recommendations

A theme that is beginning to materialize for peatlands is that the input of fresh organic matter greatly influences decomposition. Furthermore, evidence (although scarce) indicates that peat quality in Ontario's peatlands is low for microbial activity, especially those organisms involved in CH_4 cycling (e.g., Williams et al. 1998, Yavitt et al. 2000; Kuder and Kruge 2001). Changes in the quality (and quantity) of fresh organic matter inputs may regulate decomposition more than temperature and precipitation changes. However, should the successional trajectory from fens to bogs become more rapid, CH_4 production may shift from predominantly acetate fermentation to CO_2 reduction. If predicted climatic shifts are realized, coupled with vegetation that produces lower quality litter, lack of vegetation transport mode for CH_4 due to reduced sedge cover, and increases in acrotelm thickness, further reductions in CH_4 efflux from Ontario's peatlands can be expected. To more accurately understand how climate change might affect the C sink/source strength of peatlands we need (1) more complete measurements of C pools in peat, litter, and vegetation (both above- and belowground components), (2) more definitive measures of C inputs and outputs, and (3) a more comprehensive understanding of peatland C biogeochemistry. In addition, manipulative experiments involving temperature, precipitation/depth to water table,

and organic matter quality are required to improve the fundamental understanding of the relationships among important drivers in peatland C cycles. In addition, information and methodologies are needed for (1) conducting peatland inventories, (2) standardizing monitoring protocols with national and interaction initiatives, and (3) developing mechanisms to extrapolate monitoring and research results to landscape, local, regional, and provincial scales.

Another critical area for research and monitoring is the partitioning of C transport at the peatland/atmosphere/groundwater/surface water interface. This is important because a significant amount of the peatland area in Ontario borders streams and lakes. Organic matter decomposition dynamics in peatlands cause porewater to contain high concentrations of DOC, CO_2, and CH_4 that are transported to draining streams and lakes. The cycling of C in aquatic ecosystems is highly uncertain, but 20% or more of the C efflux from peatlands can be transported to surface waters and, therefore, is important to the C budget of boreal landscapes.

Those areas discussed above require attention from a research and monitoring perspective, in which the OMNR should be actively involved. An infrastructure of sites across Ontario exists that can be used to begin addressing identified research priorities. For instance, peatlands in the Hudson Bay Lowlands, which were part of the Northern Peatland Study in the late 1980s and early 1990s, the Mer Bleue Peatland Complex near Ottawa being studied under Fluxnet-Canada and the Canadian Climate Change Network, the Walley Creek forested peatland site near Cochrane, the riparian wetland study site near White River, and the Experimental Lakes Area near Kenora can serve as the initial infrastructure of study sites to begin a provincial network for studying peatland C cycling. OFRI could lead studies on forested peatlands using Walley Creek and White River sites, and collaborate with researchers at Mer Bleue and the Experimental Lakes Area. This network of sites would provide gradients for both climate (temperature and precipitation) and geology (lacustrine and marine deposits, Precambrian Shield, Ordovician Limestone). OFRI is already involved in bi-national collaboration between Canada and the United States to investigate peatland C dynamics in forested peatlands within the region. Research collaborators include scientists from the U.S. Forest Service and Michigan Technological University, with expectations that University of Minnesota and the University of Wisconsin will also become involved. The priority should be developing C budgets and determining the quality of litter and peat at each of the research sites. Results obtained from this network can be coupled with the work currently being conducted in Ontario and Canada to scale peatland C dynamics and model the importance of peatlands in C cycling in boreal landscapes using PCARS, CLASS, and C^3M (e.g., Frolking et al. 2001, 2002). Also, this network would be ideal for the developing standard methods required to study C cycling in northern peatlands.

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Appendix 1. Soil temperature, water table depth (MWAT), and average methane flux for peatlands north of 45 degrees latitude.

Peatland type	Micro-topography	Latitude (°N)	Soil temp.	MWAT	Average flux (mg m^{-2} d^{-1})	Location	Reference
Bog	nr*	45	nr	nr	20.6	Ontario	Roulet et al. 1992
Bog	nr	45	nr	nr	20.6	Ontario	Roulet et al. 1992
Bog	nr	45	nr	nr	5.8	Ontario	Roulet et al. 1992
Bog	nr	47	nr	nr	60	Minnesota	Crill et al. 1988
Bog	nr	47	nr	nr	77	Minnesota	Crill et al. 1988
Bog	nr	47	nr	nr	294	Minnesota	Crill et al. 1988
Bog	nr	47	nr	nr	218	Minnesota	Crill et al. 1988
Bog	nr	47	nr	nr	85	Minnesota	Crill et al. 1988
Bog	nr	47	nr	nr	130	Minnesota	Crill et al. 1988
Bog	nr	47	nr	nr	199	Minnesota	Crill et al. 1988
Bog	nr	47	nr	nr	89	Minnesota	Crill et al. 1988
Bog	nr	47	nr	nr	356	Minnesota	Dise et al. 1993
Bog	nr	47	nr	nr	100	Minnesota	Harriss at al. 1985
Bog	nr	47	nr	nr	306	Minnesota	Harriss at al. 1985
Bog	nr	47	nr	nr	177	Minnesota	Verma et al. 1992
Bog	Hollow	47	nr	nr	93	Minnesota	Dise et al. 1993
Bog	Hummock	47	nr	nr	21	Minnesota	Dise et al. 1993
Bog	Lawn	49	nr	-38.1	5.2	Ontario	Bubier 1995
Bog	Lawn	49	nr	-24.6	30.3	Ontario	Bubier 1995
Bog	Pool	49	nr	-4.1	156.2	Ontario	Bubier 1995
Bog	nr	54	nr	nr	0	Alberta	Vitt et al. 1990
Bog	Carpet	55	12.1	-6.4	96.9	Manitoba	Bubier et al. 1995a
Bog	Carpet	55	13.5	-9.3	86.8	Manitoba	Bubier et al. 1995a
Bog	Carpet	55	nr	-9.3	86.8	Manitoba	Bubier et al. 1995a
Bog	Hollow	55	8.4	-11.1	55.4	Manitoba	Bubier et al. 1995a
Bog	nr	55	7.2	nr	0.01104	Saskatchewan	Turetsky et al. 2002
Bog	nr	55	9.1	nr	0.04224	Saskatchewan	Turetsky et al. 2002
Bog	nr	55	11.9	nr	0.05824	Saskatchewan	Turetsky et al. 2002
Bog	nr	55	13.6	nr	0.06016	Saskatchewan	Turetsky et al. 2002
Bog	nr	55	15.4	nr	-0.0064	Saskatchewan	Turetsky et al. 2002
Bog	nr	55	19.1	nr	-0.00176	Saskatchewan	Turetsky et al. 2002
Bog	nr	55	21.1	nr	0.10016	Saskatchewan	Turetsky et al. 2002
Bog	Bog	55	21.1	-36.6	0.1	Saskatchewan	Turetsky et al. 2002
Bog	Bog	55	11.9	-44.8	0.05	Saskatchewan	Turetsky et al. 2002
Bog	Bog	55	9.1	-70.7	0.04	Saskatchewan	Turetsky et al. 2002
Bog	Bog	55	19.1	-31.2	-0.001	Saskatchewan	Turetsky et al. 2002
Bog	Bog	55	15.4	-36.5	-0.006	Saskatchewan	Turetsky et al. 2002
Bog	Bog	55	13.6	-26	-0.06	Saskatchewan	Turetsky et al. 2002
Bog	Bog	55	7.2	-30.7	-0.01	Saskatchewan	Turetsky et al. 2002
Bog	Frost mounds	55	21.9	-65	0.004	Saskatchewan	Turetsky et al. 2002
Bog	Frost mounds	55	13.6	-54.4	0.004	Saskatchewan	Turetsky et al. 2002
Bog	Frost mounds	55	8.7	-57.8	-0.02	Saskatchewan	Turetsky et al. 2002

Peatland type	Micro-topography	Latitude (°N)	Soil temp.	MWAT	Average flux (mg $m^{-2} d^{-1}$)	Location	Reference
Bog	Frost mounds	55	21.1	-39.5	0.0006	Saskatchewan	Turetsky et al. 2002
Bog	Frost mounds	55	14.4	-30.4	-0.01	Saskatchewan	Turetsky et al. 2002
Bog	Frost mounds	55	9.4	-40.2	0.01	Saskatchewan	Turetsky et al. 2002
Bog	Frost mounds	55	7.1	-40	0	Saskatchewan	Turetsky et al. 2002
Bog	Internal lawns	55	10	-19.8	0.1	Saskatchewan	Turetsky et al. 2002
Bog	Lawn	55	15.6	-18	0.4	Saskatchewan	Turetsky et al. 2002
Bog	Lawn	55	7.6	-20.4	0.6	Saskatchewan	Turetsky et al. 2002
Bog	Lawn	55	21.5	-18.8	0.01	Saskatchewan	Turetsky et al. 2002
Bog	Lawn	55	16.1	-10.3	0.02	Saskatchewan	Turetsky et al. 2002
Bog	Lawn	55	9.9	-14.8	0.06	Saskatchewan	Turetsky et al. 2002
Bog	Lawn	55	5.2	-12.2	0.06	Saskatchewan	Turetsky et al. 2002
Bog	nr	57	-7.6	nr	5	Siberia	Panikov and Dedysh 2000
Bog	nr	61	12.1	-6.5	101	Finland	Nykanen et al. 1998
Bog	nr	61	13.9	-9.2	153	Finland	Nykanen et al. 1998
Bog	nr	61	11.6	-18.9	140	Finland	Nykanen et al. 1998
Bog	nr	61	13.7	-14.2	5.2	Finland	Nykanen et al. 1998
Bog	nr	61	11.9	-23.6	6.8	Finland	Nykanen et al. 1998
Bog	nr	61	11.2	-10.3	38.6	Finland	Nykanen et al. 1998
Bog	nr	61	9.5	-20.6	19.4	Finland	Nykanen et al. 1998
Bog	nr	61	11.5	-27.8	20.9	Finland	Nykanen et al. 1998
Bog	nr	61	10.8	-31.9	8.7	Finland	Nykanen et al. 1998
Bog	nr	61	10.9	-7.1	56.4	Finland	Nykanen et al. 1998
Bog	nr	61	10.9	-11.8	21.7	Finland	Nykanen et al. 1998
Bog	nr	61	11.2	-16.6	34	Finland	Nykanen et al. 1998
Bog	nr	61	11.2	-17.1	27.5	Finland	Nykanen et al. 1998
Bog	nr	61	13	-12.6	20.6	Finland	Nykanen et al. 1998
Bog	nr	61	13.1	-18	4.2	Finland	Nykanen et al. 1998
Bog	nr	61	10.6	-26.2	16.8	Finland	Nykanen et al. 1998
Bog	nr	61	11	-30	3.7	Finland	Nykanen et al. 1998
Bog	nr	61	9.4	-17.1	10.9	Finland	Nykanen et al. 1998
Bog	nr	61	8.9	-28.9	3.3	Finland	Nykanen et al. 1998
Bog	nr	61	8.1	-38.9	6.9	Finland	Nykanen et al. 1998
Bog	nr	61	7.7	-44.7	2.1	Finland	Nykanen et al. 1998
Bog	nr	61	12.4	-7.5	46.7	Finland	Nykanen et al. 1998
Bog	nr	61	11.8	-14	61.7	Finland	Nykanen et al. 1998
Bog	nr	61	11.2	-17.5	65.4	Finland	Nykanen et al. 1998
Bog	nr	61	11.6	-2.5	158	Finland	Nykanen et al. 1998
Bog	Hollow	61	11.5	-7.2	62.5	Finland	Nykanen et al. 1998
Bog	Hollow	61	9.5	-22.1	20.1	Finland	Nykanen et al. 1998
Bog	Hummock	61	12.2	-18.7	58.6	Finland	Nykanen et al. 1998
Bog	Hummock	61	11.5	-34.5	17	Finland	Nykanen et al. 1998
Bog	Hummock	61	14.7	-1.1	106	Finland	Nykanen et al. 1998
Bog	nr	61	10.5	-24	29	NW Territories	Liblik et al. 1997
Bog	nr	61	13.5	-6	160	NW Territories	Liblik et al. 1997

Peatland type	Micro-topography	Latitude (°N)	Soil temp	MWAT	Average flux (mg $m^{-2} d^{-1}$)	Location	Reference
Bog	nr	61	16.4	-6	114	NW Territories	Liblik et al. 1997
Bog	nr	61	5.7	-35	99	NW Territories	Liblik et al. 1997
Bog	nr	63	11	nr	-0.1	Sweden	Waddington and Roulet 1996
Bog	nr	63	12.5	nr	151.7	Sweden	Waddington and Roulet 1996
Bog	nr	63	12.5	nr	2.1	Sweden	Waddington and Roulet 1996
Bog	nr	63	nr	nr	2.4	Sweden	Waddington and Roulet 1996
Bog	nr	63	nr	nr	2.4	Sweden	Waddington and Roulet 1996
Bog	nr	63	nr	nr	1.9	Sweden	Waddington and Roulet 1996
Bog	nr	63	nr	nr	0	Sweden	Waddington and Roulet 1996
Bog	nr	63	nr	nr	1.3	Sweden	Waddington and Roulet 1996
Bog	nr	63	nr	nr	4.6	Sweden	Waddington and Roulet 1996
Bog	Hollow	63	11	nr	85.6	Sweden	Waddington and Roulet 1996
Bog	Hollow	63	11.8	nr	67.6	Sweden	Waddington and Roulet 1996
Bog	Hummock	63	9.8	nr	0.9	Sweden	Waddington and Roulet 1996
Bog	Hummock	63	10	nr	1.5	Sweden	Waddington and Roulet 1996
Bog	Lawn	63	11.9	nr	42.3	Sweden	Waddington and Roulet 1996
Bog	Lawn	63	13.1	nr	36.9	Sweden	Waddington and Roulet 1996
Bog	Lawn	63	nr	nr	93.9	Sweden	Waddington and Roulet 1996
Bog	Lawn	63	nr	nr	52.9	Sweden	Waddington and Roulet 1996
Bog	Lawn	63	nr	nr	23.8	Sweden	Waddington and Roulet 1996
Bog	Lawn	63	nr	nr	93.4	Sweden	Waddington and Roulet 1996
Bog	Lawn	63	nr	nr	52.2	Sweden	Waddington and Roulet 1996
Bog	Lawn	63	nr	nr	26.8	Sweden	Waddington and Roulet 1996
Bog	Lawn	63	nr	nr	93.4	Sweden	Waddington and Roulet 1996
Bog	Lawn	63	nr	nr	42.3	Sweden	Waddington and Roulet 1996
Bog	Pool	63	12.7	nr	186	Sweden	Waddington and Roulet 1996
Bog	Pool	63	nr	nr	74.1	Sweden	Waddington and Roulet 1996
Bog	Pool	63	nr	nr	25.8	Sweden	Waddington and Roulet 1996
Bog	nr	64	8.2	nr	71.5	Alaska	Moosavi et al. 1996
Bog	nr	64	11	nr	-0.02	Alaska	Moosavi et al. 1996
Bog	nr	64	12.9	nr	289	Alaska	Moosavi et al. 1996
Bog	nr	64	13.3	nr	42.9	Alaska	Moosavi et al. 1996
Bog	nr	64	16.1	nr	-0.02	Alaska	Moosavi et al. 1996
Bog	nr	64	18	nr	407	Alaska	Moosavi et al. 1996
Bog	nr	64	nr	nr	-0.09	Alaska	Whalen and Reeburgh 2000
Bog	nr	64	nr	nr	69	Alaska	Whalen and Reeburgh 2000
Bog	nr	67	5.9	-25	-1.4	Siberia	Christensen et al. 1995
Bog	nr	67	7.1	-5	99.3	Siberia	Christensen et al. 1995
Bog	nr	68	5.6	-3	11.7	Siberia	Christensen et al. 1995
Bog	nr	68	5.8	-14	11.2	Siberia	Christensen et al. 1995
Bog	nr	68	8.2	nr	32	Sweden	Oquist and Svensson 2002
Bog	nr	68	8.9	nr	14	Sweden	Oquist and Svensson 2002
Bog	nr	69	nr	nr	28	Sweden	Oquist and Svensson 2002
Bog	nr	69	2.8	-25	1.4	Siberia	Christensen et al. 1995
Bog	nr	69	8.2	2	105.5	Siberia	Christensen et al. 1995
Bog	nr	72	3.7	-11	0.05	Siberia	Christensen et al. 1995

Peatland	Micro-	Latitude	Soil	MWAT	Average flux	Location	Reference
Bog	nr	72	4.1	2	9.8	Siberia	Christensen et al. 1995
Bog	nr	75	7.5	-17	0	Siberia	Christensen et al. 1995
Bog	nr	75	10	0	0.2	Siberia	Christensen et al. 1995
Bog	nr	75	0.03	-4	-0.2	Siberia	Christensen et al. 1995
Bog	nr	75	2.6	-4	32.2	Siberia	Christensen et al. 1995
Fen	nr	47	nr	nr	142	Alberta	Vitt et al. 1990
Fen	nr	47	nr	nr	142	Minnesota	Crill et al. 1988
Fen	nr	47	nr	nr	372	Minnesota	Crill et al. 1988
Fen	nr	47	nr	nr	325	Minnesota	Crill et al. 1988
Fen	nr	47	nr	nr	85	Minnesota	Crill et al. 1988
Fen	nr	47	nr	nr	348	Minnesota	Harriss et al. 1985
Fen	nr	47	8.4	nr	3.25	Minnesota	Shurpali and Verma 1998
Fen	nr	47	8.6	nr	3.17	Minnesota	Shurpali and Verma 1998
Fen	nr	47	9.4	nr	2.96	Minnesota	Shurpali and Verma 1998
Fen	nr	47	10.1	nr	3.04	Minnesota	Shurpali and Verma 1998
Fen	nr	47	10.7	nr	3.91	Minnesota	Shurpali and Verma 1998
Fen	nr	47	10.8	nr	4.24	Minnesota	Shurpali and Verma 1998
Fen	nr	47	11	nr	2.85	Minnesota	Shurpali and Verma 1998
Fen	nr	47	11.4	nr	2.61	Minnesota	Shurpali and Verma 1998
Fen	nr	47	12.1	nr	5.59	Minnesota	Shurpali and Verma 1998
Fen	nr	47	12.6	nr	2.83	Minnesota	Shurpali and Verma 1998
Fen	nr	47	12.7	nr	3.77	Minnesota	Shurpali and Verma 1998
Fen	nr	47	13.4	nr	2.72	Minnesota	Shurpali and Verma 1998
Fen	nr	47	13.9	nr	3.45	Minnesota	Shurpali and Verma 1998
Fen	nr	47	13.9	nr	4.84	Minnesota	Shurpali and Verma 1998
Fen	nr	47	14.6	nr	3.12	Minnesota	Shurpali and Verma 1998
Fen	nr	47	14.6	nr	6.04	Minnesota	Shurpali and Verma 1998
Fen	nr	47	14.7	nr	5.51	Minnesota	Shurpali and Verma 1998
Fen	nr	47	14.8	nr	4.25	Minnesota	Shurpali and Verma 1998
Fen	nr	47	14.9	nr	3.88	Minnesota	Shurpali and Verma 1998
Fen	nr	47	15.4	nr	4.37	Minnesota	Shurpali and Verma 1998
Fen	nr	47	15.5	nr	5.84	Minnesota	Shurpali and Verma 1998
Fen	nr	47	15.8	nr	5.88	Minnesota	Shurpali and Verma 1998
Fen	nr	47	15.9	nr	4.63	Minnesota	Shurpali and Verma 1998
Fen	nr	47	15.9	nr	5.29	Minnesota	Shurpali and Verma 1998
Fen	nr	47	16.4	nr	3.55	Minnesota	Shurpali and Verma 1998
Fen	nr	47	.	nr		Minnesota	Shurpali and Verma 1998
Fen	nr	47	nr	.		Minnesota	Shurpali and Verma 1998
Fen	nr	47	nr	.	402	Quebec	Moore and Knowels 1987
Fen	Carpet	49	nr	-2.7	61.1	Ontario	Bubier 1995
Fen	Hummock	49	nr	-25.8	3.8	Ontario	Bubier 1995
Fen	Hummock	49	nr	-32.3	2.5	Ontario	Bubier 1995
Fen	Lawn	49	nr	-14.3	32.6	Ontario	Bubier 1995

Peatland type	Micro-topography	Latitude (°N)	Soil temp.	MWAT	Average flux (mg m^{-2} d^{-1})	Location	Reference
Fen	Pool	49	nr	-1.1	34.6	Ontario	Bubier 1995
Fen	Lawn	49	nr	nr	29.3	Quebec	Moore et al. 1990
Fen	nr	53	nr	nr	17.12	Saskatchewan	Rask et al. 2002
Fen	nr	53	nr	nr	60.32	Saskatchewan	Rask et al. 2002
Fen	nr	53	nr	nr	118.72	Saskatchewan	Rask et al. 2002
Fen	nr	53	nr	nr	192.16	Saskatchewan	Rask et al. 2002
Fen	nr	53	nr	nr	321.2	Saskatchewan	Rask et al. 2002
Fen	nr	54	nr	nr	148	Alberta	Vitt et al. 1990
Fen	nr	54	nr	nr	1	Alberta	Vitt et al. 1990
Fen	nr	54	nr	nr	65	Alberta	Vitt et al. 1990
Fen	nr	54	nr	nr	24	Quebec	Moore and Knowles 1990
Fen	Carpet	54	nr	-0.3	77.4	Quebec	Bubier 1995
Fen	Carpet	54	nr	.-3	69.1	Quebec	Bubier 1995
Fen	Hummock	54	nr	-14.7	3.2	Quebec	Bubier 1995
Fen	Hummock	54	nr	-31.9	0.8	Quebec	Bubier 1995
Fen	Hummock	54	nr	-21.3	1.5	Quebec	Bubier 1995
Fen	Lawn	54	nr	-8.3	7.5	Quebec	Bubier 1995
Fen	Lawn	54	nr	-8	7.4	Quebec	Bubier 1995
Fen	Lawn	54	nr	-10	11.4	Quebec	Bubier 1995
Fen	Lawn	54	nr	-3.2	30.1	Quebec	Bubier 1995
Fen	Lawn	54	nr	-8	0.9	Quebec	Bubier 1995
Fen	Pool	54	nr	0.5	59.6	Quebec	Bubier 1995
Fen	Pool	54	nr	5	17.1	Quebec	Bubier 1995
Fen	Pool	54	nr	2.4	28.6	Quebec	Bubier 1995
Fen	Pool	54	nr	2.8	25.6	Quebec	Bubier 1995
Fen	Pool	54	nr	5.4	26.4	Quebec	Bubier 1995
Fen	Pool	54	nr	3.1	105.6	Quebec	Bubier 1995
Fen	Pool	54	nr	-0.03	16.1	Quebec	Bubier 1995
Fen	Pool	54	nr	0.3	45.6	Quebec	Bubier 1995
Fen	Pool	54	nr	2.1	90.6	Quebec	Bubier 1995
Fen	Pool	54	nr	6.6	69.2	Quebec	Bubier 1995
Fen	Pool	54	nr	0	14.5	Quebec	Bubier 1995
Fen	Pool	54	nr	0.2	9.8	Quebec	Bubier 1995
Fen	String	54	nr	-8.4	2.3	Quebec	Bubier 1995
Fen	String	54	nr	-8.8	6.6	Quebec	Bubier 1995
Fen	String	54	nr	-12.6	7	Quebec	Bubier 1995
Fen	String	54	nr	-15.9	6	Quebec	Bubier 1995
Fen	String	54	nr	-13.8	4.3	Quebec	Bubier 1995
Fen	String	54	nr	-14.5	0.4	Quebec	Bubier 1995
Fen	Pool	55	nr	nr	33	Alberta	Vitt et al. 1990
Fen	nr	55	nr	nr	2.83	Manitoba	Moosavi and Crill 1997
Fen	Carpet	55	.	-2.2	92.3	Manitoba	Bubier 1995
Fen	Carpet	55	11.1	-8.1	60.6	Manitoba	Bubier et al. 1995a

Peatland type	Micro-topography	Latitude (°N)	Soil temp.	MWAT	Average flux (mg m^{-2} d^{-1})	Location	Reference
Fen	Carpet	55	11.8	-11.2	108.3	Manitoba	Bubier et al. 1995a
Fen	Carpet	55	12.4	-2.2	92.3	Manitoba	Bubier et al. 1995a
Fen	Carpet	55	14.3	-9.6	55.3	Manitoba	Bubier et al. 1995a
Fen	Carpet	55	nr	-8.1	60.6	Manitoba	Bubier et al. 1995a
Fen	Carpet	55	nr	-9.6	55.3	Manitoba	Bubier et al. 1995a
Fen	Hollow	55	nr	-7.7	60.5	Manitoba	Bubier 1995
Fen	Hollow	55	nr	0.1	16.3	Manitoba	Bubier 1995
Fen	Hollow	55	6.8	0.1	16.3	Manitoba	Bubier et al. 1995a
Fen	Hollow	55	12.5	-7.6	76.8	Manitoba	Bubier et al. 1995a
Fen	Hollow	55	13.7	-7.7	60.5	Manitoba	Bubier et al. 1995a
Fen	Hummock	55	5.4	-20.1	19.1	Manitoba	Bubier et al. 1995a
Fen	Hummock	55	9.1	-30.4	5.7	Manitoba	Bubier et al. 1995a
Fen	nr	55	nr	nr	7.5	Quebec	Moore and Knowles 1990
Fen	nr	55	nr	nr	30.5	Quebec	Moore et al. 1990
Fen	nr	55	nr	nr	72	Quebec	Moore et al. 1990
Fen	nr	55	nr	nr	30	Quebec	Moore et al. 1990
Fen	nr	55	nr	nr	18	Quebec	Moore et al. 1990
Fen	nr	55	nr	nr	48	Quebec	Moore et al. 1990
Fen	nr	61	8.2	-30.1	-0.3	Finland	Nykanen et al. 1998
Fen	nr	61	12.6	-5.9	323	Finland	Nykanen et al. 1998
Fen	nr	61	8.4	-39.7	0.2	Finland	Nykanen et al. 1998
Fen	nr	61	9.7	-8.3	140	Finland	Nykanen et al. 1998
Fen	nr	61	9.1	-32	-0.3	Finland	Nykanen et al. 1998
Fen	nr	61	10.4	-32.8	22.6	Finland	Nykanen et al. 1998
Fen	nr	61	8.9	-48.3	-0.4	Finland	Nykanen et al. 1998
Fen	nr	61	13.6	-2.2	345	Finland	Nykanen et al. 1998
Fen	nr	61	12.4	-7.3	192	Finland	Nykanen et al. 1998
Fen	nr	61	9.2	-42.5	-0.6	Finland	Nykanen et al. 1998
Fen	nr	61	6.9	-41.3	-0.5	Finland	Nykanen et al. 1998
Fen	nr	61	9.8	-45.4	-3.5	Finland	Nykanen et al. 1998
Fen	nr	61	13.1	-15.3	84.9	Finland	Nykanen et al. 1998
Fen	nr	61	11.5	-13.1	119.3	Finland	Nykanen et al. 1998
Fen	nr	61	10.7	-27.5	20.9	Finland	Nykanen et al. 1998
Fen	nr	61	14.7	-5	163	NW Territories	Liblik et al. 1997
Fen	nr	61	13.6	-9	132	NW Territories	Liblik et al. 1997
Fen	nr	61	16.1	-4	221	NW Territories	Liblik et al. 1997
Fen	nr	61	15.4	-4	145	NW Territories	Liblik et al. 1997
Fen	nr	61	12.4	-14	47	NW Territories	Liblik et al. 1997
Fen	nr	61	11.1	-9	58	NW Territories	Liblik et al. 1997
Fen	nr	61	11.4	-9	81	NW Territories	Liblik et al. 1997
Fen	nr	61	13.2	-8	65	NW Territories	Liblik et al. 1997
Fen	nr	61	11	-35	12	NW Territories	Liblik et al. 1997
Fen	nr	61	10.9	-23	18	NW Territories	Liblik et al. 1997
Fen	nr	61	12	-17	23	NW Territories	Liblik et al. 1997

Peatland type	Micro-topography	Latitude (°N)	Soil temp.	MWAT	Average flux (mg m^{-2} d^{-1})	Location	Reference
Fen	nr	61	12.4	-14	23	NW Territories	Liblik et al. 1997
Fen	nr	61	5.5	-39	0.5	NW Territories	Liblik et al. 1997
Fen	nr	61	8.5	-43	7	NW Territories	Liblik et al. 1997
Fen	nr	62	nr	nr	76.8	Finland	Saarnio et al. 1997
Fen	Lawn	62	nr	nr	251.2	Finland	Saarnio et al. 1997
Fen	Flark	67	9.8	2	45	Russia	Heikkinen et al. 2002
Fen	Flark	67	9.8	5	65	Russia	Heikkinen et al. 2002
Fen	Flark	67	9.8	6	80	Russia	Heikkinen et al. 2002
Fen	Flark	67	9	9	40	Russia	Heikkinen et al. 2002
Fen	Flark	67	10.1	-2.5	20	Russia	Heikkinen et al. 2002
Fen	Flark	67	10.1	-2	50	Russia	Heikkinen et al. 2002
Fen	Flark	67	10.1	-2	52	Russia	Heikkinen et al. 2002
Fen	Flark	67	10.1	-2	60	Russia	Heikkinen et al. 2002
Fen	Flark	67	10.1	-1	80	Russia	Heikkinen et al. 2002
Fen	Hummock	67	9.5	-20	0	Russia	Heikkinen et al. 2002
Fen	Hummock	67	9.5	-16	0	Russia	Heikkinen et al. 2002
Fen	Hummock	67	9.5	-15	0	Russia	Heikkinen et al. 2002
Fen	Hummock	67	9.5	-13	0	Russia	Heikkinen et al. 2002
Fen	Hummock	67	9.5	-10	0	Russia	Heikkinen et al. 2002
Fen	Hummock	67	9.5	-8	10	Russia	Heikkinen et al. 2002
Fen	Lawn	67	9.2	-6	20	Russia	Heikkinen et al. 2002
Fen	Lawn	67	9.2	-4	40	Russia	Heikkinen et al. 2002
Fen	Lawn	67	9.2	-3	35	Russia	Heikkinen et al. 2002
Fen	Lawn	67	9.2	-4	60	Russia	Heikkinen et al. 2002
Fen	Lawn	67	9.2	-4	65	Russia	Heikkinen et al. 2002
Fen	Lawn	67	8.3	-6	0	Russia	Heikkinen et al. 2002
Fen	Lawn	67	8.3	-6	0	Russia	Heikkinen et al. 2002
Fen	Lawn	67	8.3	-4	0	Russia	Heikkinen et al. 2002
Fen	Lawn	67	8.3	-4	15	Russia	Heikkinen et al. 2002
Fen	Lawn	67	8.3	-6	45	Russia	Heikkinen et al. 2002
Fen	nr	68	6.1	11.8	290	Siberia	Nakano et al. 2000
Fen	nr	68	6.1	12.3	271	Siberia	Nakano et al. 2000
Fen	nr	68	4.2	-15.8	-0.7	Siberia	Nakano et al. 2000
Fen	nr	68	4.2	-14.8	-0.5	Siberia	Nakano et al. 2000
Fen	nr	68	7.8	nr	87	Sweden	Oquist and Svensson 2002
Fen	nr	68	8.3	nr	60	Sweden	Oquist and Svensson 2002
Fen	nr	68	nr	nr	322	Sweden	Oquist and Svensson 2002
Forested	nr	64	nr	-10	10	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-10	0	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-4	1	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-4	20	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-4	50	Alaska	Moosavi et al. 1996

Peatland type	Micro-topography	Latitude (°N)	Soil temp.	MWAT	Average flux (mg $m^{-2} d^{-1}$)	Location	Reference
Forested	nr	64	nr	-4	50	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-8	175	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-10	75	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-10	125	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-10	160	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-10	115	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-10	125	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-12	160	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-12	110	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-6	10	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-10	20	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-10	30	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-12	60	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-14	45	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-18	80	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-26	90	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-28	65	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-30	45	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-40	35	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-40	30	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-34	35	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-36	30	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	-38	45	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	nr	-0.02	Alaska	Moosavi et al. 1996
Forested	nr	64	nr	nr	-0.02	Alaska	Moosavi et al. 1996
Marsh	nr	45	nr	nr	1.2	Ontario	Roulet et al. 1992
Marsh	nr	45	nr	nr	0.5	Ontario	Roulet et al. 1992
Meadow	nr	64	nr	nr	4.88	Alaska	Whalen and Reeburgh 1988
Meadow	nr	68	nr	nr	14	Alaska	Schimel 1995
Meadow	nr	68	nr	nr	22.27	Alaska	Schimel 1995
Meadow	nr	68	nr	nr	27.47	Alaska	Schimel 1995
Meadow	nr	68	nr	nr	28.13	Alaska	Schimel 1995
Meadow	nr	68	nr	nr	36.93	Alaska	Schimel 1995
Meadow	nr	68	nr	nr	63.2	Alaska	Schimel 1995
Meadow	nr	68	nr	nr	87.33	Alaska	Schimel 1995
Meadow	nr	68	nr	nr	87.47	Alaska	Schimel 1995
Meadow	nr	68	nr	nr	87.87	Alaska	Schimel 1995
Meadow	nr	68	nr	nr	101.1	Alaska	Schimel 1995
Meadow	nr	68	nr	nr	136.8	Alaska	Schimel 1995
Meadow	nr	68	nr	nr	158.8	Alaska	Schimel 1995
Meadow	nr	68	nr	nr	200.4	Alaska	Schimel 1995
Meadow	nr	73	3.6	0	34.2	Siberia	Christensen et al. 1995
Meadow	nr	73	1.6	-25	0	Siberia	Christensen et al. 1995
Sedge	nr	47	nr	nr	644	Minnesota	Harriss et al. 1985

Peatland type	Micro-topography	Latitude (°N)	Soil temp.	MWAT	Average flux (mg $m^{-2} d^{-1}$)	Location	Reference
Swamp	nr	45	nr	nr	7.1	Ontario	Roulet et al. 1992
Swamp	nr	45	nr	nr	0.15	Ontario	Roulet et al. 1992
Swamp	nr	45	nr	nr	0.2	Ontario	Roulet et al. 1992
Swamp	nr	45	nr	nr	0.2	Ontario	Roulet et al. 1992
Swamp	nr	45	nr	nr	1.2	Ontario	Roulet et al. 1992
Swamp	nr	45	nr	nr	0.25	Ontario	Roulet et al. 1992
Swamp	nr	45	nr	nr	69.3	Ontario	Roulet et al. 1992
Swamp	nr	45	nr	nr	0.4	Ontario	Roulet et al. 1992
Swamp	Hummock	49	nr	-37.8	5.9	Ontario	Bubier 1995
Swamp	Hummock	49	nr	-42.1	0.5	Ontario	Bubier 1995
Swamp	Lawn	49	nr	-22.5	19.2	Ontario	Bubier 1995
Swamp	Lawn	49	nr	-26.8	3.2	Ontario	Bubier 1995
Swamp	Pool	49	nr	-2.6	109.1	Ontario	Bubier 1995
Tundra	nr	68	8.2	-25	6.8	Siberia	Christensen et al. 1995
Tundra	nr	68	9.3	-4	85.6	Siberia	Christensen et al. 1995
Tundra	nr	69	4.9	-25	-1	Siberia	Christensen et al. 1995
Tundra	nr	69	6.7	-8	102.7	Siberia	Christensen et al. 1995
Tundra	nr	69	3.6	-25	-0.06	Siberia	Christensen et al. 1995
Tundra	nr	69	3.7	-25	0	Siberia	Christensen et al. 1995
Tundra	nr	70	0.5	-25	2.4	Siberia	Christensen et al. 1995
Tundra	nr	71	0.5	nr	46.3	Siberia	Nakano et al. 2000
Tundra	nr	71	0.8	nr	0.3	Siberia	Nakano et al. 2000
Tundra	nr	72	3.6	1	21.5	Siberia	Christensen et al. 1995
Tundra	nr	72	4	-25	0.9	Siberia	Christensen et al. 1995
Tundra	nr	72	2	-25	15.2	Siberia	Christensen et al. 1995
Tundra	nr	72	2.3	-25	44.9	Siberia	Christensen et al. 1995
Tundra	nr	74	16.6	nr	-0.02	Greenland	Christensen et al. 2000
Tundra	nr	74	16.3	nr	-0.01	Greenland	Christensen et al. 2000
Tundra	nr	74	16.1	nr	-0.01	Greenland	Christensen et al. 2000
Tundra	nr	74	14.8	nr	0.01	Greenland	Christensen et al. 2000
Tundra	nr	74	17.5	nr	-0.01	Greenland	Christensen et al. 2000
Tundra	nr	74	15.3	nr	-0.04	Greenland	Christensen et al. 2000
Tundra	Continuous	74	13.2	-1.3	12.7	Greenland	Christensen et al. 2000
Tundra	Continuous	74	13.1	0.9	2.8	Greenland	Christensen et al. 2000
Tundra	Continuous	74	12	3.6	11.4	Greenland	Christensen et al. 2000
Tundra	Continuous	74	14.5	2.5	11.7	Greenland	Christensen et al. 2000
Tundra	Continuous	74	14.1	4	3.7	Greenland	Christensen et al. 2000
Tundra	Continuous	74	15	0.2	10.5	Greenland	Christensen et al. 2000
Tundra	Grassland	74	14.4	-0.1	2.7	Greenland	Christensen et al. 2000
Tundra	Grassland	74	15.8	-3.5	5.7	Greenland	Christensen et al. 2000
Tundra	Grassland	74	16.5	-3.7	0.1	Greenland	Christensen et al. 2000
Tundra	Hollow	74	15.5	-4	11.6	Greenland	Christensen et al. 2000
Tundra	Hollow	74	14.9	0.6	9.1	Greenland	Christensen et al. 2000
Tundra	Hollow	74	15.1	-1.1	15.5	Greenland	Christensen et al. 2000

Peatland type	Micro-topography	Latitude (°N)	Soil temp.	MWAT	Average flux (mg $m^{-2} d^{-1}$)	Location	Reference
Tundra	Hollow	74	14.5	1.2	2.9	Greenland	Christensen et al. 2000
Tundra	Hollow	74	13.9	3.4	4.4	Greenland	Christensen et al. 2000
Tundra	Hollow	74	14.7	4.2	11.1	Greenland	Christensen et al. 2000
Tundra	Hummock	74	15.6	-10.1	3.1	Greenland	Christensen et al. 2000
Tundra	Hummock	74	16.3	-10.4	3.7	Greenland	Christensen et al. 2000
Tundra	Hummock	74	15.7	-11	2.5	Greenland	Christensen et al. 2000
Tundra	Hummock	74	15.4	-14.4	0.7	Greenland	Christensen et al. 2000
Tundra	Hummock	74	15.1	-8.7	1.8	Greenland	Christensen et al. 2000
Tundra	Hummock	74	15.6	-7.5	5.3	Greenland	Christensen et al. 2000
Tundra	Salix	74	14.1	-6.5	0	Greenland	Christensen et al. 2000
Tundra	Salix	74	15.6	-16.4	-0.01	Greenland	Christensen et al. 2000
Tundra	Salix	74	14.1	-25.3	0.01	Greenland	Christensen et al. 2000
Tundra	nr	75	4.2	-25	0.7	Siberia	Christensen et al. 1995
Tundra	nr	75	5.7	0	155.1	Siberia	Christensen et al. 1995
Tundra	nr	76	0.7	-7	1.3	Siberia	Christensen et al. 1995
Tundra	nr	76	2	-1	0.2	Siberia	Christensen et al. 1995
Tundra	nr	77	0.5	-8	0.05	Siberia	Christensen et al. 1995
Tundra	nr	77	3.1	1.8	0.03	Siberia	Christensen et al. 1995
Tussock Tundra	nr	64	-2	nr	100	Alaska	Whalen and Reeburgh 1988
Tussock Tundra	nr	64	-15	nr	0	Alaska	Whalen and Reeburgh 1988
Tussock Tundra	nr	64	-10	nr	0	Alaska	Whalen and Reeburgh 1988
Tussock Tundra	nr	64	-15	nr	0	Alaska	Whalen and Reeburgh 1988
Tussock	nr	64	-15	nr	0	Alaska	Whalen and Reeburgh 1988
Tussock	nr	64	-10	nr	0	Alaska	Whalen and Reeburgh 1988
Tussock	nr	64	2	nr	0	Alaska	Whalen and Reeburgh 1988
Tussock	nr	64	10	nr	0	Alaska	Whalen and Reeburgh 1988
Tussock	nr	64	15	nr	20	Alaska	Whalen and Reeburgh 1988
Tussock	nr	64	15	nr	90	Alaska	Whalen and Reeburgh 1988
Tussock	nr	64	12	nr	80	Alaska	Whalen and Reeburgh 1988
Tussock	nr	64	5	nr	60	Alaska	Whalen and Reeburgh 1988
Tussock	nr	64	1	nr	43	Alaska	Whalen and Reeburgh 1988
Tussock	nr	64	-15	nr	115	Alaska	Whalen and Reeburgh 1988
Tussock	nr	64	-20	nr	0	Alaska	Whalen and Reeburgh 1988
Tussock	nr	64	nr	nr	8.05	Alaska	Whalen and Reeburgh 1988
Tussock	nr	64	nr	nr	0.62	Alaska	Whalen and Reeburgh 1988
Tussock	nr	64	nr	nr	0.47	Alaska	Whalen and Reeburgh 1988

* nr = not reported